Colombo Stefanie (Orcid ID: 0000-0003-1828-7145)
Roy Koushik (Orcid ID: 0000-0001-7205-9034)
Mraz Jan (Orcid ID: 0000-0003-3545-1269)
Wan Alex H L (Orcid ID: 0000-0003-1703-3725)
Tibbetts Sean (Orcid ID: 0000-0001-5509-4081)
Øverland Margareth (Orcid ID: 0000-0003-1142-6624)
Metian Marc (Orcid ID: 0000-0003-1485-5029)

Toward achieving circularity and sustainability in feeds for farmed blue foods

Stefanie M. Colombo[1*], Koushik Roy[2], Jan Mraz[2], Alex H. L. Wan[3], Simon Davies[3], Sean M. Tibbetts[4], Margareth Øverland[5], David S. Francis[6], Melissa M. Rocker[6], Laura Gasco[7], Emma Spencer[8], Marc Metian[9], Jesse T. Trushenski[10], Giovanni Turchini[11]

[1]Department of Animal Science and Aquaculture, Faculty of Agriculture, Dalhousie University, Truro, Nova Scotia, Canada, B2N 5E3

[2]Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in České Budějovice, Na Sádkách 1780, 370 05, Ceske Budejovice, Czech Republic

[3]Aquaculture and Nutrition Research Unit, Carna Research Station, Ryan Institute and School of Natural Sciences, University of Galway, Carna, Connemara, Co. Galway, Ireland, H91 V8Y1

[4]Aquatic and Crop Resource Development Research Centre, National Research Council of Canada, Halifax, NS, Canada

[5]Department of Animal and Aquacultural Sciences, Faculty of Biosciences, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

[6]Nutrition and Seafood Laboratory, School of Life and Environmental Sciences, Deakin University, Queenscliff 3225, VIC, Australia

[7]Department of Agricultural, Forest and Food Sciences, University of Turin, Largo P. Braccini 2, 10095 Grugliasco, TO, Italy

[8]Global Ecology Lab, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

[9]International Atomic Energy Agency–Marine Environment Laboratories (IAEA-MEL), Radioecology Laboratory, Principality of Monaco, Monaco

[10]Riverence Holdings LLC, 604 W Franklin St Boise, ID, 83702, USA

[11]School of Agriculture and Food, Faculty of Veterinary and Agricultural Sciences. The University of Melbourne, 3010, VIC, Australia.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/raq.12766

Abstract

The aims of this review are to describe the role of 'blue-food production' (animals, plants and algae harvested from freshwater and marine environments) within a circular bioeconomy, discuss how such a framework can help the sustainability and resilience of aquaculture and to summarize key examples of novel nutrient sources that are emerging in the field of fed-aquaculture species. Aquaculture now provides >50% of the global seafood supply, a share that is expected to increase to at least 60% within the next decade. Aquaculture is an important tool for reducing resource consumption in global protein production and increasing resilience to climate change and other global disruptions (i.e., pandemics, geo-political instability). Importantly, blue foods also provide essential nutrition for a growing human population. Blue foods are helping to help the global goal of 'zero hunger' (United Nation's Sustainable Development Goal 2) while reducing the dependency on finite natural resources but further refinement and new solutions are needed to make the industry more 'circular' and sustainable, particularly with respect to sourcing raw materials for aquafeeds. This review describes the feed resources that are available or may be created within a circular bioeconomy framework, their role within the framework and in aquaculture, and ultimately, how these resources contribute to de-risking and establishing a resilient aquaculture production chain.

Keywords: Aquaculture, circular economy, fisheries, insects, scavenger, sustainability

Introduction

Current and anticipated effects of climate change are compounding the inadequacies of the global food system, whereby the productivity of natural and agricultural ecosystems is threatened by a warming climate, more frequent and severe droughts, floods, and other extreme weather events, ocean acidification and so forth. Moreover, the COVID-19 pandemic and recent geo-political instability in Eastern Europe have revealed the complexity and fragility of raw material and perishable product supply chains. Collectively, these factors are forcing society to reconsider the state of our global food system and seek ways to increase its resilience. Blue foods — animals, plants and algae harvested from freshwater and marine environments — supply protein to over 3.2 billion people[1]. Aquaculture currently contributes approximately half of the blue foods produced[2], and thus is a powerful tool for increasing food security:

- Aquaculture can relieve harvest pressure on capture fisheries, allowing for stock rebuilding and adoption of climate-sensitive fishery management plans[3];
- Aquaculture is a diverse enterprise with many species and rearing systems, allowing for seafood to be produced closer to consumers[3];
- Aquatic livestock are substantially more efficient than terrestrial livestock and can be raised with fewer feed inputs, less freshwater use, and a smaller carbon footprint[4].

Among the blue foods, aquaculture of fed farmed fish represents the majority[2], and thus is the focus of this review. Despite the relevance of aquaculture and other blue foods to improving the security and climate resilience of the global food system, seafood is one of the most perishable and widely traded commodities in the world[3], therefore the distribution network is energy-intensive and vulnerable to supply chain disruptions. Thus, for aquaculture to fully realize its potential as a means of doing more with less in food production, one must consider both the associated opportunities and threats. As aquaculture continues to grow, so does the requirement for environmentally sustainable and cost-effective aquafeeds as demand is expected to increase to ~87 million tonnes by 2025 [5]. It is imperative to rethink uses of commonly used ingredients and actively develop new raw materials for use in aquafeeds. In doing so, there must be consideration for (over)reliance on finite natural resources, effects on ecosystem functionality and continued provision of ecosystem services, and the potential for countering climate change or mitigating its effects. Aquaculture has become the largest consumer of global fishmeal (FM) and fish oil (FO) supplies, accounting for 68% and 89% of annual production, respectively [6]. In response to economic and sustainability concerns, over the past 20 years the aquaculture sector has made considerable progress in reducing FM and FO inclusion rates and using marine resources more judiciously[7]. As a result, most modern commercial aquafeeds are now predominantly composed of terrestrial plant materials and animal by-products [8]. The industry's reliance on marine-origin raw materials has shifted to terrestrial feedstuffs, and aquaculture now indirectly assumes many of the inputs and externalities associated with terrestrial agriculture, such as freshwater use, deforestation and other types of habitat modification, areal footprint, pesticide and fertilizer use, irrigation, and nutrient run-off leading to aquatic pollution [9,10]. Without mindful, comprehensive consideration of a feed formulation's total environmental cost, one risks trading the ecological consequences of one ingredient type for another with equal or greater impacts, thereby diminishing aquaculture's ability to add resilience to the global food system[11].

Besides these concerns, many of the terrestrial plant ingredients present certain nutritional challenges for farmed aquatic species [8]. Plant-based diet compositions tend to be higher in carbohydrates, lower in protein, low (if any) omega-3 (n-3) long chain polyunsaturated fatty acids (LC-PUFA) and contain antinutritional factors (ANFs). Carnivorous fish are evolutionarily and metabolically adapted for high protein (>40%) and high-fat diets (>15%), with low carbohydrate tolerance. Aquafeeds generally contain more protein and lipid than terrestrial animal feeds and are much lower in carbohydrates; these differences are accentuated for the very nutrient-dense feeds produced for carnivorous fish species. Diets with greater than 20% digestible carbohydrates tend to reduce growth in the animal, as well as show hyperglycemia after intake of a carbohydrate-enriched meal; therefore, in general, carnivorous fish are considered glucose-intolerant [12]. Furthermore, most plant oils are somewhat limited in their ability to replace FO in diets for fish that require LC-PUFA, as they completely lack n-3 LC-PUFA [13]. Typically, they are rich sources of n-6 and n-9 FA, mainly 18:2n-6 and 18:1n-9, except for some oilseeds that may contain significant levels of 18:3n-3. Although considered excellent sources of digestible energy, feeding terrestrial plant oils inevitably lowers levels of the n-3 LC-PUFA in the diet. Another challenging aspect of including plant products in fish diets is ANFs, which can cause adverse effects on digestion, absorption, and decreased ability to utilize macronutrients [14]. Several ANFs have been identified and associated with detrimental effects on growth performance and health when using vegetable-based diets in aquafeeds [15]. As a result, feeds that are primarily terrestrial plant-based (especially for carnivorous fish) can have physiological impacts on digestibility and nutrient utilization, growth, intestinal integrity, gut enteritis and health, immune response to stress and pathogens, reproductive success, and early ontogeny survival [8]. In summary, there is a need to prohibit the use of non-sustainable marine feed ingredient sources (e.g., derived from over exploited and/or non-sustainably managed wild-caught marine fish, crustaceans, mollusks, and aquatic plant species) and non-sustainable terrestrial feed ingredient sources (particularly the use of non-deforestation/ conversion-free feed ingredients, as well as highly subsidized imported feed ingredient sources)[16].

Climate change and other constraints will undoubtedly challenge the future growth of marine aquaculture [17,18]. Aspects and consequences of climate change that directly affect marine aquaculture include increasing temperature and sea-level rise, shifts in precipitation patterns, freshening from glacier melt, acidification, and other changes in ocean conditions, productivity, currents and other cycles; increasing occurrence of extreme weather events, eutrophication, and changing distributions of pathogens, parasites, and invasive/nuisance species [18–20]. Many of these factors also affect freshwater aquaculture, along with increased competition for freshwater resources. Indirectly, climate change can impact aquaculture via aquafeed supplies, for example, hampering the ability to produce crops in extreme and increasingly unpredictable conditions and jeopardizing the long-term sustainability of marine products (i.e., FM and FO) harvesting. Furthermore, significant transformations are needed within terrestrial crop and livestock agriculture production to reduce GHG emissions and shift agriculture from a carbon source to a carbon sink which currently exacerbates the climate scenario [21]. Aquaculture should remain aware of its reliance on other primary food production; however, aquaculture is also a means of taking existing production and waste products and transforming it into high-quality food with a lower carbon footprint compared to other means of food production[4]. Environmental change and increasing seafood demand and harvest pressure jeopardizes the current capacity for marine fisheries to support the food and nutrition security of individual nations [22], thereby affecting wild-caught fish for human consumption as well as the FM and FO supply. The contribution from aquaculture to climate change and mitigation/remediation strategies (ecological and carbon footprints, life cycle assessment (LCA), blue growth initiative) will be critical for blue food production in the future [18]. Environmental performance assessed in a broad context is key for assessment and improvements and informing sustainable diets[4].

Furthermore, the resiliency of food production, in general, is needed in the face of other global stressors, such as the COVID-19 pandemic and geo-political instability. The pandemic has affected food security, in terms of availability, access, utilization, and stability. The situation imposed a serious threat to global food security, such as labor shortages created by restrictions (e.g., movements of people, quarantine restrictions, temporary scale backs or shutdowns), shifts in food demand, and export restrictions that have disrupted trade flows for staple food commodities [23]. Food price and stability is particularly important for food security among the poorest and most marginalized populations. Therefore, it is key that aquaculture contributes to high food output in order to make the food supply (and cost) less volatile[11]. Thus, considering aquaculture within the circular bioeconomy framework is a strategic and resilient way forward for the industry, without exhausting resources that are already subject to so many external pressures. The supply, cost, environmental sustainability, and social acceptability of raw materials for aquafeeds are under significant consideration and scrutiny. This has consequences not only for the outcome of aquafeed production, but also for global aquaculture economic viability, environmental sustainability, and social license to operate. As a result, the industry must incorporate and/or develop innovative practices that involve conservation, restoration, and/or remediation. This presents new opportunities for the next-generation of protein and lipid sources for aquafeed that will be more resilient and consistent in production, which is important in a changing world, and somewhat unstable society.

The field of fish nutrition has been evolving since at least the early 1900s[24,25]. From their infancy, The evolution of commercial aquafeed raw materials from being mostly FM and FO-based, to becoming primarily terrestrial-based, which is the current aquafeed and could be termed 'Aquafeed 2.0', has occurred rapidly; essentially within the last 20 years [26]. It is time now to develop and transition to 'Aquafeed 3.0'. Ultimately, the supply, cost, environmental sustainability, and social acceptability of raw materials for aquafeed are considered vulnerable. This uncertainty in the global supply chain can have a direct impact on aquaculture production and sustainable practices.

This review describes the role of aquaculture within a circular bioeconomy, how the framework can help the sustainability and resiliency of aquaculture and summarizes key examples of novel (and existing) nutrient sources that are on the cusp of defining Aquafeed 3.0.

Circular bioeconomy framework and its relevance in aquaculture nutrition

The concept – Circular Bioeconomy Framework (CBF)

By definition, circularity means recycling and reusing wastes from one system as inputs for another system. Waste is not trash but can often be considered a co-product and a resource in circularity. 'Bioeconomy' is a concept coined by the European Commission in 2012 to address the possibilities of the conversion of renewable biological resources into economically viable products and bioenergy[27]. The circular bioeconomy aims to improve resource use efficiency (RUE), minimize environmental footprint, and avoid losses by design, reuse, recycle, remanufacture, and reintegration of non-food grade resources as much as possible [28–30]. In a circular bioeconomy, the circular part aims to maintain the value of land, products, materials, and resources for as long as possible. The bio-economy part targets renewable biological resources to produce food, materials, and energy [29,31]. Circularity demands a paradigm shift in thinking, changing focus from increasing productivity (presently) to increased resource use efficiency (future)[32]. The application of CBF in food production systems is not only aimed at waste valorization or minimization of losses; it can also include: (a) a reduced food-feed conflict for future generations; (b) upcycling of biomass losses or organic waste streams to the human food chain; (c) degrowth strategies and de-prioritizes luxury use; (d) preservation of biodiversity and ecosystem services in local food systems; (e) eco-intensification strategies rather than linear intensification; (f) strong symbiosis or resource use complementarities (exchanges) locally or regionally ("agri-aqua-food system"); (g) expanding the scope of environmental impact assessments to the greater "agri-aqua-food system" and covering all categories of planetary health boundary framework. A synopsis in this regard can be found in numerous studies[29,33–44]. A case example of agri-aqua-food system symbiosis (*i.e.,* CBF in aquaculture) is depicted in Fig 1. Therefore, adoption of this approach is expected to simultaneously address multiple issues at once: food security, managing natural resources sustainably, reducing dependencies on non-renewable resources, mitigating climate change, and creating jobs [31,32]. The definition and practice of the CBF is still evolving [30,34,45].

History of circularity in aquafeeds

The idea of circularity in aquafeeds has been practiced for decades, with using by-products or non-consumed (by human) biomasses of animal and plant origin[46,47]. As animal production, including aquaculture, intensified within an equally evolving regulatory system (e.g., legislations of animal welfare, food safety or environmental regulations), many of the by-products became highly competitive (e.g., oilseed cakes) while some by-products were partly restricted (e.g., animal rendering by-products). Most by-products are of crude quality, so they must be processed and refined before inclusion in aquafeeds For 'semi-intensive' pond fish farming at lower trophic levels, less refined circular ingredients of plant-origin can be used directly to complement and supplement natural food availability (e.g., ponds culturing carp, tilapia, or catfish). Less refined by-products can be fed to ponds, and the wasted nutrients or uneaten feed can be upcycled to farmed fish biomass through improved productivity of the pond's food web (zooplankton, zoobenthos, algae)[48,49]. This practice has been undertaken for decades in pond systems. On the other hand, in intensive systems, such as recirculating aquaculture systems, only refined and high-quality by-products, often with higher cumulative energy consumption and environmental footprint, can be used. Traditional, yet effectively, farm-made feeds can more easily achieve CBF in production in pond systems; however, many are not as practical in other systems. Applying the CBF in aquafeeds (considering various systems for fed finfish species) will require such considerations.

Need for CBF in modern aquafeeds

Conclusions from most LCAs highlight feed and feeding efficiency as fundamental to the environmental impact of most aquaculture production systems [50–54]. In fact, several aquaculture LCAs highlight that feeds 'solely' contribute to most LCA impact categories [42,55–57]. Therefore, applying the principles of CBF to aquafeeds would have far-reaching consequences for farmed blue foods, making them truly qualified for a proposed planetary healthy diet. Most current aquafeeds have shifted from primarily using marine-based ingredients as the source of protein and fat (Aquafeed 1.0) to terrestrial -based ingredients (Aquafeed 2.0) and is generally considered as a more sustainable way forward for aquafeed production. However, there are other issues regarding conventional plant-based feedstuffs which may be counter-productive in a future circular bioeconomy framework. These issues include high eutrophication potential (directly linked with digestibility of fed aquatic animals, fertilizers use in land-based cultivation of plant feedstuffs), high land occupation potential (linked with land-based cultivation), and high ecotoxicity potential lined with pesticide reliant agricultural practices) surrounding decisions to switch entirely to ‘presumably sustainable’ plant-based choices in aquafeed [58]. The alternative feedstuffs of plant origin that are presently being referred to as ‘sustainable’ (but may not be so[28]) are also known to contain anti-nutritional factors, nutritional imbalances, and non-bioavailable form(s) of specific nutrients. This may decrease digestibility of the feed and subsequently increase excretory nutrient loading from fish to the environment [59,60].

CBF in aquafeed or circular aquafeed concept (Aquafeed 3.0) is necessary to amend these pitfalls. In this context, plant-, algal-, microbial- and insect- feedstuffs are raised on byproducts, integrated with the existing farming systems (such as bio-based waste recycling, end-of-pipe treatments) and producing biomass that does not go for direct human consumption (avoiding food-feed conflict) would be the face of future, circular origin, and sustainable fish nutrition sources in aquaculture. The current narrative around FM and FO-use may be re-considered in terms of ‘net impact’ when a complementary set of feedstuffs are combined (which also may include recovered fishery and aquaculture products); in many cases, the use of a modest amount of FM/ and/or FO, coupled with other locally sourced, circular origin ingredients may yield a smaller environmental footprint than feeds that are devoid of marine resources. A balance is needed to maximize fish performance and to improve environmental performance for the next evolution of aquafeeds.

Going from sustainable (present) to circular (future) aquafeed concept

The first formulated, extruded pellets for fish (i.e., Aquafeed 1.0) were manufactured mostly with FM and FO, which have long served as ‘gold standards’ for the aquaculture nutrition industry[61]. Over the last two decades, a major area of research has focused on FM and FO replacements/alternatives. As a result, from the time of review of 2000 [47] to 2021 [7], the use of FM and FO has considerably decreased in aquafeed [62]. Modern aquafeeds are now predominantly composed of terrestrial plant materials and animal by-products; and the use of FM and FO has been significantly reduced to even negligible amounts (≤10%) for omnivorous and herbivorous fish species like carp and tilapia [61]. But it must be clarified that despite reduced inclusion rates of FM/ FO, the fed aquaculture production and parallelly production of aquafeed have increased also [62]. Therefore, the industry-wide use of FM/ FO has stayed the same.

Some of these alternative feedstuffs to FM and FO are also not without environmental impact and not all of them fit the principles of circularity. For example, some FM and FO alternatives add pressure on land and water resources, have food-feed conflicts, do not valorize any waste, or have their own environmental footprints [28,30]. For example, a heavy reliance on terrestrially derived agriculture products has sustainability issues, as mentioned in the previous section. Many plant-based aquafeed ingredients, often promoted as sustainable to FM and FO, may also directly compete with human food streams [28]. In circular agriculture or aquaculture, it is referred to as food-feed conflict (from a human perspective) [29,63]. For example, EAT-Lancet commission’s planetary healthy diet guidelines suggest consumption of at least

125 grams of dry beans, lentils, peas, and other nuts or legumes per day; but consuming no more than 98 grams of red meat (pork, beef, or lamb), 203 grams of poultry, and 196 grams of fish per week[21]. In comparison, global average of unprocessed red meat consumption is 357 grams per week [38], *i.e.,* 3.5 times excess. If planetary healthy diet recommendations of EAT-Lancet commission are to be strictly followed, many plant protein concentrates should be directly entered into the human food chain, as the decrease in consumption of animal protein (red meat) must be supplemented by another protein source (plant protein). With the advent of bioengineered or fabricated plant-based foods mimicking meat (e.g., Beyond Meat®, Impossible Foods®), many of the plant protein concentrates/ isolates presently used in aquafeed (e.g., pea, canola, lupine, fava bean, sunflower, cereal gluten, soy proteins, etc.) pose future food-feed conflict. As such, plant protein concentrates, even if derived from agricultural by-products (e.g., middling, broken pieces), might be antagonistic to the CBF. This is where 'Aquafeed 2.0' probably stands today – at a crossroad between *status quo* (plant-based sustainable) or toward the CBF. In this context, plant-, algal-, microbial- and insect- feedstuffs which are raised on agri-aqua-food system wastes[41], and rendered animal/ fish by-products that do not go for direct human consumption (avoiding food-feed conflict)[64,65] would be ideal future, circular feedstuffs and will likely be part of the evolution from 'Aquafeed 2.0' to 'Aquafeed 3.0'. Some opportunities to achieve Aquafeed 3.0 'locally' are given in Table 1.

However, many of these ingredients remain largely untested in fish. Their current use (even on the experimental scale) in ruminants and poultry may be encouraging, but the benefits to fish may still differ due to different gastrointestinal and nutritional physiology. For example, the crude protein content (as derived from Kjeldahl-N) of some circular-origin feedstuffs (e.g., grass protein) may be misleading as they contain a relatively high proportion of non-protein nitrogen (NPN) relative to nitrogen from amino acids[66]; only ruminants can use NPN effectively. In pursuit of novel avenues for sourcing circular-origin feedstuffs, there can be some epidemiological and anti-nutritional risks too. Previous global epidemic contagions have originated from within food systems [55,56]. Dealing more with circular-origin feedstuffs and using them in aquaculture feeds might increase such risks. There are obvious health hazards in recycling food system waste streams as feed for aquaculture[67,68]. For 'semi-intensive' pond fish farming at lower trophic levels, less refined circular ingredients of plant-origin may be used directly to complement and supplement natural food base fluctuations [49]. But for intensive aquaculture, some of the circular-origin feedstuffs may be less-refined (high ash, high fibers on original matter basis), which require a significant degree of processing before use to avoid anti-nutritional factors and improve bioavailability of certain nutrients.

In the CBF, re-focusing resource and material flows from global scales to regional/local scale is necessary. However, one of the most challenging issues and risks of the CBF relates to logistics. Even if ingredients sourced through the CBF may help lower the environmental footprint of aquafeeds, shipping feed ingredients around the globe will result in carbon emissions and is expensive, which can tear the sustainability of the CBF[69]. Supply issues may result if feed producers rely on ingredients from other parts of the world (even if they are sourced from the CBF). While transportation plays a critical role in virtually all agricultural supply chains, recent problems with restriction of global movement of containers containing consumer goods also illustrates the problem[70]. Logistics and infrastructure are also an impediment to capture and recovery of processing fishery byproducts, and there is usually global shipment involved[71]. These barriers have been well-studied with few solutions proposed, however, prioritizing the local economy, both for the acquisition of its feedstock and for the offer of its products, will help de-risk the CFB[69]. Depending on the species, life stage, and system, localizing the CBF may be more realistic and attainable immediately. A good example of this is "farm made feeds" for semi-intensive pond systems which often valorizing local circular resources. For decades, Asian carp culture in ponds have practiced and stressed the importance of such approach[72].

Scoping of novel and non-traditional sources for Aquafeed 3.0

There are emerging examples of byproducts that could be utilized in the CBF to create novel aquafeed ingredients. While more work needs to be done to validate these potential resources (particularly regarding safety and consistency), they could provide a useful source of nutrients for producing downstream products described in this review, such as insects or single cell organisms. For example, supermarket or retail chain waste, including fruits and vegetables, bread products, meat, and fish. Many of these waste streams are refined and edible and some of the biomass of consumable foods can still be used for direct human consumption[68,72]. However, beyond this, some of the waste stream byproducts can be used as a protein, carbohydrate, or fiber sources that could be useful in the CFB[73–76]. There are also waste/co-products from food and beverage production, such as from the sugar industry by-products (sugar extracted beet-root pulp)[77] and spent brewery or distillery wastes (e.g., yeast, malt sprouts, spent brewers grains)[78–80]. Some ingredients which could be circular source of additives such as spent coffee grains, fruit and vegetable byproduct[73,81]. Besides providing nutrients for downstream ingredient production (e.g., insects, single cell organisms), some examples could be used directly as carbohydrates, which may act as prebiotics, binders, and improve pellet quality. Finally, forest co-products (such as wood residue, sawdust, etc.) can be used to grow yeast and mycoproteins as an aquafeed protein source[82], or used as functional additives (such as lignin), that can improve gut microbiota and growth, as well as pellet quality[83,84].

Linking 'Aquafeed 3.0' with scavenger ecology concept

The CBF is inspired from nature-based solutions[29]. The demands and tolerances of some aquaculture species, particularly carnivores, make their nutrition and feeding more challenging than for other livestock—ecologically speaking, they are specialists with relatively narrow trophic roles in nature. There is limited opportunity to modify the nutritional physiology of cultured fish (e.g., selective breeding programs can improve tolerance of plant-based ingredients among carnivorous fish, but the selected fish remain carnivorous in a behavioral, anatomical, and more-or-less physiological sense), one can carefully process plant-based ingredients and formulate largely vegetarian feeds to fit within the nutritional tolerances of carnivorous species. Indeed, decades of research and on-farm application have demonstrated that carnivorous fish do not require animal-based feeds and can be raised on diets that reflect a much more cosmopolitan diet than would be observed in nature. Further, if one considers the diversity of aquaculture species together— thinking of the industry collectively as a single 'organism' in the 'ecosystem' of global food production, one can envision aquaculture as a generalist 'scavenger' able to shift among niches and to utilize feed resources opportunistically. Thus, there is both intraspecific and interspecific flexibility that can be exploited to increase circularity in raw material sourcing and aquaculture nutrition. If aquaculture must be a scavenger of terrestrial food system waste streams, some inspirations and knowledge from nature are prudent to discuss. This links together the concept of scavenger ecology and Aquafeed 3.0. Within the biosphere, humans may appear to be the only species often relying on finite resources, in their utopian attempt to step aside from the boundaries of the circular essence of nature itself. Most contemporary food production systems have not differed significantly during their expansion phases but are now facing the need to consider circularity [85]. For many fed-aquaculture species, the primary sources of nutrients used in their feeds are wild-caught fish [86]. However, when realizing the finite nature of such resources, aquaculture has evolved towards the use of plant-based nutrient sources. Consequently, this has significantly shifted the effective trophic level of the industry and the culture species themselves [26].

This observation prompted us to make a reflection on aquaculture evolution based on an analogy in which we could compare aquaculture, and its role within the global food systems, to a hypothetical carnivorous species and its role within its ecosystem. When this given hypothetical species (aquaculture) had been facing a limited availability of preys (fish meal and fish oil), it had to modify its feeding behavior towards other available resources (terrestrial agricultural products). However, in this rapid (and forced) evolution, triggered by limited resource availability, from a carnivorous to an omnivorous, almost herbivorous status, aquaculture appears to have skipped the first, and most logical and effective step implemented by carnivorous animals in the wild when facing food shortages: adapting to a scavenger feeding pattern. Accordingly, continuing to draw on this analogy, we believe there is merit in exploring the basic principles of scavenger ecology and their role in healthy ecosystems, so that this could be mimicked by aquaculture within contemporary food production systems.

In nature, scavengers are organisms that feed on decomposing organic matter, including dead or dying plants and animal carcasses. They include a suite of vertebrate and invertebrate species, and comprise an important, but often forgotten functional group in terrestrial and aquatic ecosystems [87,88]. Scavengers play a key role in intact ecosystems as "waste removalists". Exclusion studies (whereby scavengers are prevented access to carcasses) have demonstrated that both vertebrate and insect scavenging can dramatically reduce carcasses persistence time in the environment [87,89]. By removing decomposing organic matter scavengers fulfil an important ecosystem function, reducing disease spread that can result from microorganisms associated with decomposition [90]. Scavenging also contributes to energy dispersal and accelerated nutrient cycling throughout environments (e.g., through their feces; [91]). By dispersing nutrients across multiple trophic levels, scavengers help to stabilize food webs, sometimes to a greater extent thanthat of predators [88]. Despite the apparent functional importance, however, scavenging has been overlooked in many conventional food webs, and studies have downplayed or failed to consider the dietary importance of decomposing organic matter for many species.

While some animals have evolved as "obligate scavengers" that rely entirely on decomposing organic matter, such as old and new world vultures (Families: Cathartidae and Accipitridae) and burying beetles (Sub-family: Nicrophorinae), almost all carnivorous and many omnivorous organisms engage in opportunistic scavenging behaviour [92]. These species, known as "facultative scavengers", differ in terms of what and how often they scavenge. Their tendency to scavenge also differs across varying environments and conditions. For example, scavenging propensity may be increased by elevated carcass availability following mass mortality events, such as after wildebeest and salmon migration events [93,94], or due to widespread anthropogenic hunting practices [95]. Animals may also place greater reliance on scavenging when alternative resources are low in availability, e.g., during severe winters when small mammal numbers decline [96]. Periods of low food resources can even encourage scavenging behaviour by otherwise herbivorous animals like the snowshoe hare (*Lepus americanus*) [97].

Scavengers serve an important role, linking otherwise disconnected food webs and helping to maintain nutrient and energy cycles in functioning ecosystems. Aquaculture could serve a similar role in the food production 'ecosystem', opportunistically 'scavenging' raw materials from various agricultural and food processing sectors and reintegrating non-food grade resources into the production of high quality human foods. Thus, applying what is known about scavengers and similarly opportunistic species might provide insight in to how aquaculture might be best-positioned to improve the circularity of global food systems. Embracing the principal of opportunistic scavenging by utilization of non-food grade and otherwise underutilized products and acting as 'waste removalists' would serve well since most high value aquaculture species are carnivores. The sourcing of raw materials possessing superior nutritional qualities compared to plants and co-products would have more efficacy in the food chain. However, this will open to important considerations with respect to what feed can be used and how. Learning from the knowledge of scavenger ecology, we know that the quality of the decomposing organic matter will further dictate whether organisms feed preferentially on it. Nutrient composition, as well as size and condition, are important factors dictating scavenger community structure and scavenging activity [98,99]. For aquaculture, the quality of the organic biomass available will dictate whether it could be utilised in aquafeed, as is or after some form of processing. Further, continuing the observation of knowledge from scavenger ecology, it is known that certain species may scavenge exclusively during earlier or later decomposition stages, or avoid particular types of decomposing organic matter, such as the carcasses of carnivorous species [100].

Facultative scavengers that do not rely solely on decomposing organic matter for nutrients do not typically share the same high efficiency in detection and consumption of this food resource as obligate scavengers. They are, however, generally more ubiquitous in the landscape and in some systems and continents, such as Australia, and may be the only scavenging organisms present in certain taxonomic groups (e.g., vertebrates).In aquaculture, not all biomasses can be used at any time, and risks associated with vectoring pathogens or contaminants should be cautiously considered. At the same time, not all cultured aquatic species will likely be able to use the same biomass in their feed as some are more frugal and able to adapt to a variety of food items, such as some freshwater, tropical lower-trophic species like tilapias[101], whilst others have a reduced ability to accept feed containing different raw materials, such as some marine top-order predator finfishes, like yellow tail kingfish[102].

Last, and still learning from scavenger ecology knowledge, the reliance that scavengers have on decomposing organic matter as an alternative resource during food shortages or difficult environmental conditions may have a considerable effect on their population dynamics [103,104]. In turn, this may also influence the interactions that they have with other species in the surrounding environment, such as their prey (if they also act as predators; [105]) or their predators (if they are the prey of other animals [91]). Consistently, considering aquaculture within the border food systems, the availability and the cost-effectiveness of biomasses might fluctuate overtime relative to variable trends in primary production due to markets or environmental changes, but also affected by other competitor users, for example, biofuels and the pet food industry. These macro-dynamics will of course affect the availability of such nutritional resources for the aquaculture sector, which would benefit by increasing its nutritional flexibility towards increased resilience and improved adaptability.

Concluding this analogy, as much as scavengers are essential in healthy and sustainable ecosystems, when aiming at healthy and sustainable global food systems, there is a need for a sector to play this scavenger role. Accordingly, we believe that aquaculture has such potential, which can be achieved by embracing circularity in the origin and supply of raw materials used in aquafeed.

Recovery of protein and oil from seafood waste

The use of FM and FO derived from capture fisheries has allowed aquaculture to grow annually at a rate of 6.9 % attaining 114.5 million tonnes in 2018 [106]. However, the use of recovered marine proteins and oils from seafood waste streams in wild capture fisheries and aquaculture is somewhat an under-appreciated resource. These can include parts of the fish and shellfish that are not directed into the human food chain or unintentionally caught species. This could form an integral part of the circular seafood production system. This can particularly be advantageous as these ingredients can deliver the essential nutrients (e.g., specific AAs, FAs, vitamins, pigments, and trace elements) that other regenerated ingredients and other traditionally used non-marine ingredients may lack, such as plant by-products.

There are many different sources of fisheries and aquaculture waste streams that could be recovered for aquafeed use and form part of the circular aquafeed concept. For instance, within Europe, the Landing Obligation was introduced as part of the Common Fishery Policy (Regulation (EU) No 1380/2013) to address the issue of bycatch. This is also known as discards, where undersized individuals, low value, or unintentional fish and shellfish species are caught while fishing for targeted species. The landing obligation is set out to prevent the catch from being disposed into the sea. While, within the United States, it has been estimated that 1.93 million tonnes of fish and invertebrates were discarded from 2010 to 2015 [107]. As such, there are sufficient quantities of seafood waste that would make the valorisation process a commercially viable operation.

Furthermore, the production of trimmings/waste (e.g., viscera, fatty trims, heads, skin, tail, and blood) from fish processing can have a financial burden on processors due to the need for compliant waste disposal methods, e.g., dedicated treatment plants or within the EU category 2 and 3 compliant animal byproduct renderers [108]. For example, Atlantic cod produces 50% trimming waste plus the associated processing water and can cost £60 per tonne for its disposal [109]. Or the disposal cost of lobster by-products can cost AUD $150 per ton [110]. For crustaceans, the processing of whole animals yields waste streams such as the shell, gonads, gills, and digestive tract. Furthermore, the processing of crustaceans to extract the meat out (i.e., deshelling) can typically leave residue proteins and oils in the extremities. While the amounts are low from each animal being processed, the quantity of protein that could be recovered could be substantial when the industry is taken as a whole, or the number of crustaceans being processed within a processing plant. For example, it has been estimated that around 18,000 tonnes of Argentine red shrimp (*Pleoticus muelleri*) processed waste were discarded annually in Patagonia, of which 1,950 tonnes of proteins and 93 tonnes of n-3 LC-PUFA could be recovered [111].

In certain incidences, these processing waste streams can go onto rendering plants that are subsequently cooked, de-oiled, and dried to produce fish protein meals for pet foods, terrestrial animal feeds, and aquafeeds [108]. In comparison, the regeneration of trimmings from farmed fish into FM and FO is also carried out. However, the differences are that the latter waste stream is often prohibited in its use in organic status aquafeeds (e.g., EU Commission Regulation (EC) 710/2009) or being fed back to the same farmed species over the concerns of disease transfer, e.g., salmon waste fed back to salmon [112]. The quantity of protein and oil that can be recovered can be substantial, however, for example, 35-41.5% of the harvested Atlantic salmon can go to waste post-trimming [108,113]. In 2019, it has been estimated that 2,586,890 tonnes of farmed salmon were harvested globally [106]. Therefore, taking a conservative approach could lead to a potential figure of 905,411 tonnes (wet weight) of salmon waste being produced annually (i.e., 2,586,890 x 0.35), with the possibility of being regenerated as FM and FO for non-salmonid aquafeeds and terrestrial animal feeds. The interest in exploiting these waste products has broadened to other industries including the production of bioplastics and biopolymers [114] and biogas production [115], which might pose as a competitor for the waste stream in the near future.

The canning industry can also offer another substantial and underexploited protein and oil resource for aquafeed production. For example, the sardine and mackerel canning industry generates large amounts of protein and oil-rich wastewaters: cook water and stickwater from the cooking, handling, canning, and can washing processes. It has been estimated that the tuna canning industry suffers from a 45 % or higher in waste during the processing, cooking, and canning stages [116]. These waste streams have the potential to be dewatered through heating or utilising newer technologies such as reverse osmosis, nano-filtration, or spray drying to create a highly digestible proteinaceous feed ingredient containing soluble proteins, peptides, and free AAs and preserving heat-liable compounds, e.g., antioxidants [117]. For the recovery of oil, there are several methods that have been proposed for separating and refining the oil from the wastewater including centrifuging and pH shifting to the newer methods in supercritical extraction [118].

The hydrolysing of whole fish and shellfish is widely used to create both human foods (e.g., soup bases, stocks, and meat fillers) and health supplements (e.g., muscle building and protein replacement). Commercial-scale hydrolysis typically uses an enzymatic approach (exogenous or autolytic) such as protease to give a high degree of control over the quality of the final products: oil, solid mineral (from bones), oil-protein emulsion, soluble protein hydrolysate, and partially soluble protein hydrolysate [119]. Depending on the extent of the hydrolysis process, the yield of each fraction can vary but also create hydrolysate products that have functionality and bioactivity. The latter attributes can add value to the aquafeed, for example, fish protein hydrolysates are known to possess antioxidative properties that can play a role in stabilising the finished diet. Or the smaller peptides (e.g., di- and tri- peptides) found in the hydrolysates can be employed for specific feed utilisation properties such as palatability, growth performance enhancers, and immune promotion [120]. The application of hydrolysis technology can allow a more effective recovery in proteins and oils from fisheries and aquaculture waste streams when compared to traditional FM and FO production methods, i.e., mincing, cooking, and separating. The hydrolysation process can break down indigestible fibrous proteins such as keratin, collagen, and chondrin that are found prevalent in scales, skin, cartilage frames, and gills waste streams. Secondly, the processing can liberate proteins that would otherwise be bound to the bones in fish and chitin in crustaceans [110]. Together with the increasing biotechnological know-how and economically viability of using exogenous enzymes, protein hydrolysis is now becoming more prevalent in the recovery of nutrients from fisheries and aquaculture.

Besides protein and oil recovery from fisheries and aquaculture processing waste, crustaceans (i.e., shells) can also be exploited to produce glucosamine, chitin and chitosan derivative products. These functional ingredients have many positive attributes which are well studied in farmed animals for their ability to induce antimicrobial, growth-promoting, antioxidant activity, leaner meat quality, prebiotic, and immune-stimulatory effects [121]. Similarly, the waste shells could be extracted for the bound astaxanthin and other important marine carotenoids, as high-value feed additives used in aquafeeds for the pigmentation of skin and flesh in salmonids, tilapia, crustaceans, and ornamental fish species. An array of processing technologies has been tested and validated to achieve a viable quantity of astaxanthin including solvent extraction, supercritical fluid extraction, fermentation, and enzyme hydrolysis [122]. However, a commercially feasible method of extraction will have to be economically competitive with current market products that are produced either synthetically, or from krill, microalgae, and terrestrial plants [123]. The recovery of calcium can also be achieved from the bone of fish [120], and mollusc shell waste that can be used as an aquafeed additive [124].

The use of fisheries and aquaculture waste streams is not new to aquafeed with low value FM and blended FO being extensively exploited for many commercial farmed species. However, many of these end products are at the lower end of the market, and the opportunities and potentials are not fully realized. The application of state-of-the-art biorefinery processing such as hydrolysis, and fermentation can do more than just enhance nutrient bioavailability. It can produce new functional properties to the fisheries and aquaculture waste stream offering higher added value. More importantly, to fully exploit seafood waste as a circular aquafeed ingredient, logistical and economical barriers must be overcome. This can relate to the issue of transporting highwater content and highly perishable seafood waste to a centralized render/processor, which can incur significant transport costs. Some processors produce seafood waste in low quantities or produced infrequently which is not enough to be economically viable for collection and processing, e.g., fishmongers. A coordinated and incentivized approach is required to capture and utilize these waste streams, e.g., sustainability certification (ecolabeling) for circular economy aquafeed ingredients, and life cycle analysis to show environmental impact reduction[125].

Terrestrial animal by-products

Terrestrial animal by-products (ABP) generally consist of animal parts considered unsuitable for human consumption, and include organs, fat, skin, feet, abdominal and intestinal contents, bone, and blood. In the US and EU alone, more than 40 million tonnes of ABP are produced per annum [126], equating to a range of meal and oil products such as meat and bone (M&B) meal, blood meal, poultry offal meal (POM), processed animal proteins (PAP, poultry by-product oil (PbO), and tallow (TAL). The majority of terrestrial ABP originate from lamb, cattle, pig and chicken, with the associated edible (for livestock, but not for human consumption) by-products representing approximately 17-35% of the live animal weight, respectively [127–129]. Although these by-products are considered unfit for direct human consumption, their utilisation as a potential substitute for limited resources within aquafeeds is a viable, circular, and environmentally sustainable option.

For ABP to enter the feed industry and become part of the circular economy, they must first be converted into stable, usable products. Rendering is the combination of heat, time and pressure to stabilise raw materials, evaporate the water content and ensure sterilization [130,131]. ABP can be dry rendered, where raw materials are heated in a steam-jacket vessel, or wet rendered, where steam is injected directly into the rendering tank with the raw materials [131,132]. During the rendering process, moisture is removed and fats are released by draining and pressing for refinement [131,132]. The remaining material ("crax") is processed into the final meal product following additional moisture removal and grinding. POM is generally rendered between 100-125°C and M&B meal is rendered at 135-140°C, for approximately 40-90 minutes [129,131,132]. Three types of blood meal exist based on the drying process, however, spray-drying is the most advantageous for blood meal as it is evaporated in a low temperature vacuum (49°C) and sprayed into a hot air stream (316°C), allowing for minimal impact on proteins and subsequent digestibility [132]. Once ABP have been rendered, they are a safe and generally nutritious component for animal feeds.

Given their high nutritional value and comparably low cost, ABP are of significant value to the aquafeed and aquaculture industries [133–135] and is especially true of poultry byproduct meal (PBM) and feather meal that is widely employed. Nutritionally, in comparison to plant-based meals ABP are high in crude protein (50-80%), have high energetic content (crude lipids), contain a range of vitamins and trace minerals (e.g., B12, iron, cobalt, selenium), and are generally free from, or low in, anti-nutrients and indigestible complex carbohydrates [14,132,136,137]. Generally, ABP meals and oils are a good source of EAA and FA, respectively [129,132,137,138], however, the specific composition depends on the animal of origin and associated animal parts composing the raw material and the processing conditions [130,139,140]. For example, POM has an essential AA profile that closely resembles that of FM when compared to terrestrial plant-based meals [138,141], whilst M&B meal can have a relatively well-balanced AA profile with a slight methionine and/or tyrosine deficiency [132,141]. Comparatively, blood meal has a poorly balanced AA profile with relatively high leucine and lysine content and significant isoleucine and methionine deficiencies [132,141]. Notably, makes blood meal an ideal supplementary protein to use in combination with plant-based meals that are low in lysine content [142]. PbO and TAL are nutritionally viable supplementary lipid sources given their high levels of oleic acid [129]. PbO also has low saturated FA content, while TAL has a balanced saturated FA and monounsaturated FA content with very low levels of n-6 polyunsaturated FA; however, both PbO and TAL lack the coveted FAs EPA and DHA that are found in fish oil [129,143,144]. However, evidence suggests an increased deposition efficiency of these health promoting FAs in fish when fed diets rich in SFA and MUFA sources (e.g., TAL) are included in dietary formulations [145].

The only significant limitations surrounding APB utilisation are regulatory in nature. Biologically, there are very few limitations, particularly in comparison with other aquafeed ingredients. That said, optimizing the use of ABP in aquafeeds still presents a challenge to the industry. ABP composition is highly variable, particularly that of meals (e.g., POM, M&B meal) [134,140]. For example, high ash content or deficiencies in particular AA (e.g., lysine, methionine and tryptophan) in meals, or high levels of SFA in oils, can limit the use of ABP within aquafeeds as these factors can have a negative impact by reducing protein and lipid digestibility [146,147]. Albeit less than 100% digestibility is an expectation for all protein sources and is readily managed—the same should be true for lipid sources high in saturated fats[148]. Not only are ABP influenced by species of origin (e.g., poultry versus cattle) and condition of the animal (e.g., age and gender) [149], but also by slaughterhouse operations and rendering processes (e.g., individual plants and batches, raw material freshness, rendering temperature) [140,150,151]. The nutritional quality of ABP is directly linked to the presence and bioavailability of AAs and FAs in the respective meal and oils [140,144,152,153]. These profiles can become further degraded prior to rendering through raw material freshness and microbial contamination [139,140], or during rendering due to excessive processing conditions (e.g., extreme heat, prolonged cooking duration) [130,140,151]. For example, lysine availability within meals decreases with increasing processing temperatures [154]. As such, proximate composition, as well as AA and FA compositions, must be closely monitored to optimize the use of these products in aquafeed formulations [134,140].

A range of studies have examined a continuum of ABP inclusion levels across a range of farmed aquaculture species [155–158]. Dietary inclusion recommendations are associated with the specific ABP (e.g., type of meal, species of origin), as well as individual farmed species or species groups being fed. POM has one of the best overall AA profiles of land animal by-products and is recommended at a general inclusion rate of 5-25% for fish and crustaceans [141]. Studies have found high protein digestibility and performance across a range of species and trophic levels, including carp and salmonids [150,151,159,160]. M&B meal also has a well-balanced AA profile and has been recommended at a 10-15% inclusion rate due to potentially high ash content [129]. Growth and performance metrics are reported as comparable to plant-based meals when M&B meal was included in aquafeeds for tilapia and hybrid striped bass [161,162], whilst protein digestibility of M&B meal was relatively high in rainbow trout [163]. Conversely, blood meal is recommended at <10% inclusion as the AA content is imbalanced, palatability issues have been observed, and processing conditions (e.g., temperature and method of drying) can significantly affect energy content and digestibility [129,141,164]. PbO and TAL have been recommended at a dietary inclusion rate of inclusion rate 5-10% [129] due to good growth performance and high feed palatability [144,165,166], however, reduced digestibility of TAL at low temperatures requires further assessment [144,146,158]. As such, given the various strengths and weaknesses associated with each ABP source, mixing, and matching of ABP in unison with the addition of other nutritional components is paramount. Taking this approach, the nutritional and energetic profiles can be optimized whilst facilitating the utilization of a myriad of by-product ingredients that would otherwise go to waste.

In recent times, regulatory considerations have complicated the use ABP aquafeed, largely dependent on the farming region. As an example, the use of ABP in feedstuffs in Australia is high compared to its use in the European Union[167]. Lower levels of ABP in Europe can be attributed to strict regulations introduced in 1994 which banned the use of processed animal proteins for cattle and sheep, that in 2000, was extended to include all farmed animals (Council Decision 2000/766/EC). However, since 2006 blood products from non-ruminants have been authorized for use in aquaculture (Commission Regulation (EC) No 1292/2005), whilst in 2013 the EU re-authorized processed animal proteins derived from healthy non-ruminant farmed animals (i.e., mainly pigs and poultry) to be used in aquafeed (Commission Regulation (EU) No 56/2013). This protein source, termed Processed Animal Protein (PAP) is produced from Category 3 material which is deemed fit for human consumption at the point of slaughter (REF). Although ruminant processed animal proteins are still prohibited in feeds for all food producing animals, proposals for ruminant gelatin in non-ruminant feed have been under consideration (Commission Regulation (EU) No 1372/2021) as the EU moves towards goals of waste reduction and a more circular bioeconomy. As such, consumer acceptance of aquaculture products fed ABP is now one of the final hurdles for ABP inclusion in aquafeeds. Notably, consumer acceptance or rejection is typically driven by negative sensory properties of the final product (distaste), harmful consequences (perceived danger), or negative ideation (knowledge of the origin or nature of the product) [168,169]. Clarity is therefore required to inform the public that perceived risks (e.g., BSE) are not an issue in aquaculture final products, and that highlighting the circular bioeconomy of ABP in aquafeeds may mitigate negative ideation of aquaculture final products.

Insects

Triggered by economic and environmental concerns relative to the use of conventional raw materials such as FM, FO, other animal-based ingredients and soybean meal, insects are attracting exponentially increasing research attention for their potentials as novel ingredients in aquaculture[170–174]. The growing interest in these innovative resources is associated with their valuable nutritional composition in terms of protein quantity (from about 25 to 75% dry matter) and quality (biological value and balanced EAA provision), lipids, vitamins, minerals and bioactive compounds, such as chitin, antioxidant peptides, short chain FA, antimicrobial peptides, which are able to exert positive effects on the health status of aquaculture species [175–178]. However, among 2,111 recorded edible insect species for food and feed [179], only a few possess a real potential for feed purposes. Indeed, to be considered for this purpose, mass scale production is needed to deliver the large, and quality-consistent, quantities of insect meal expected by market. To date, this process is fully established only for a very limited number of insect species. The processed meals derived from two Diptera, the black soldier fly (*Hermetia illucens*), and the common housefly (*Musca domestica*), and from one Coleoptera, the yellow mealworm (*Tenebrio molitor*), seem to be the most promising [173,177,180]. The life cycles of these three species are all characterized by a larval stage, which is the phase ideally suited for the meal production. The length of the larval stage is related to the environmental conditions (with temperature being the main factor, and usually considered optimal around 25 to 30°C) and the composition of the rearing substrate. This last parameter is important because even if insects are well known to be able to grow in low nutrients substrates, as for all animals, optimal performances are obtained using balanced diets able to match the animal nutritional requirements [181,182]. In addition to these three species which are the more established and currently utilised for aquafeed, other species are currently under investigation as novel nutrient sources. Among them, are the field cricket (*Gryllus bimaculatus*) [183–185], the house cricket (*Acheta domesticus*) [186], and the super mealworm (*Zophobas morio*) [187–190], which appear to be the most promising. Moreover, in China and India, sericulture delivers significant quantities of silkworm (*Bombix mori*) pupae, considered waste products of this industry and their use as feedstuff can represent a valuable method to mitigate some of the environmental impacts of silk production [191].

The utilisation of insect larvae derived products in aquafeed, and particularly those from larvae of dipteran species, represent an excellent example of the circular economy. From their hatching, larvae can feed and grow on a wide range of organic biomasses, bio-converting and accumulating the residual nutrients into high value proteins, lipids, and other compounds with excellent attributes [192–194]. For the black soldier fly, Pinotti & Ottoboni[195] reported a concentration of about 2.1 to 2.8 of protein and 5 times of the lipids from the substrate to the insect biomass through the bioconversion process. It is important to acknowledge that many of these raw materials are already used directly in animal feeds, including aquaculture feeds. For this to work from a circularity perspective, use of feedstocks with no direct use in animal feeding would be most appropriate.

Different organic substrates have been tested for insect rearing, ranging from plant to animal by-products or waste [193,195–197]. Dry substrates such as cereal left over, are preferred by coleopteran species while dipteran require a moisture content of about 65% and therefore wet food is more suitable, although use of freshwater should be a consideration here. Worldwide insects are seen as a potential instrument for waste management solving both waste and nutrient (protein) issues. The use of food and agricultural waste as grow-out substrate is a key factor for the insect industry with a circular economy perspective [197,198]. However, as the European Union is concerned, insects are labeled as “farmed animals” and therefore can only be fed in accordance with general animal feed law[194,199]. This poses limits on the sector development and potential long term economic viability. If reared on non-otherwise valorised side-streams, insects are manifestly more sustainable than most of the other protein sources [192,200–202]. They do not enter direct competition for food with other livestock and are highly efficient in converting feed mass into body mass [192]. Compared to terrestrial crops, insects have shorter production cycles, and require lower water inputs and land area to produce the same yield of protein [203].

The insect nutrient content depends on the species, the life stage and on environmental parameters such as temperature or substrate composition used for larvae grow-out and light [177,178,193]. Keeping in mind the metabolism of each species, which favors the synthesis of specific FAs, the available literature agreed on the influence of the rearing substrate on the lipid fraction of resulting larvae, both in terms of quantity and FA composition. Terrestrial insects do not naturally contain LC-PUFA such as EPA and DHA, reflecting the terrestrial ecosystem lacking these FA. The use of substrates containing these FA enables their accumulation in larvae. Likewise, the breeding substrate influences the mineral and vitamin fraction of the final product [204–208]. However, while macronutrient composition (including total protein content), is related to insect composition and the quantity of nutrients in the substrate, amino acid (AA) composition is inconsistent in the literature. In fact, some studies reported an impact of the substrate on AA composition [209], while others argue that these components are poorly modulated, as they are under genetic regulation and more uniform in profile [177,178,193,208]. Variability found on the AA composition is likely linked to different life stages considered during research. In general, insects are rich in fat, and in raw larvae the total lipid content is higher than the content of conventional feedstuff they intend to substitute in aquafeeds, such as FM and soybean meal [177,178]. High lipid levels could lead to oxidation process (rancidity), decreasing the shelf life and the quality of the meal. Therefore, insect producers currently apply defatting processes to partially decrease the lipid content of resulting in insect-derived meals, aiming at lipid levels ranging from 4% to about 18% (DM) [210,193,177]. The result of the defatting process is a more stable product with a high protein content. As for most rendering processes, it is important to underline how the methodologies and parameters applied in the production of insect-derived products (i.e. temperature, pressure, type of solvent) can have significant impacts on the protein and lipid recovery and on the quality of the product by influencing not only the composition, but also the color, texture, flavor and therefore its acceptability by fish [210–212].

The number of studies assessing insect-derived meals and oils in aquafeeds has been growing exponentially in the last ten years. Trials mainly investigated the stock performance and nutrient digestibility [183,185,213–222] and the impact on final product quality [223,224]. The impact of insect-derived products on fish heath status and microbiota composition is an emerging topic of interest [225–231]. Moreover, there are innovative aspects such as myogenesis-related gene expression [232] or methionine pathway [233] that would provide an in depth understanding of the interaction between the insect-based feed and the farmed aquatic animal. Recent literature reviews are available [173,176,180,234]. Insect-derived products can also find application in Pacific white shrimp (*Litopenaeus vannamei*) culture resulting in good performances [235–238], and improved survival rates and reduced immunosuppression when shrimps had to face infection [239]. As far as insect meals used as protein sources in aquafeeds are concerned, a recent meta-analysis performed by Hua, (2021) underlined how the "replacement level" concept was not an appropriate parameter in assessing the nutritive values of alternative ingredients and that the "level of inclusion" concept was more objective [171]. Accordingly, insect meals are a good match for fish protein needs and can be included up to 40-60% in aquafeeds without impairing performances. Another recent meta-analysis performed by Weththasinghe et al.[234] showed that feeding salmonids black solider fly larva (BSF) did not affect growth performance or protein digestibility or utilization. However, the effect of BSF inclusion depended on the type of protein source(s) replaced, where replacement of fishmeal with BSF had a negative impact and replacement of non-fish meal sources had a positive effect on growth performance.

Concerning digestibility, some research has highlighted a reduction in values with the increasing level of insect meal inclusion. The commonly accepted reasons for this is that the exoskeleton is not very digestible. For example, the N-acetyl glucosamine main constituent of chitin often results in over estimation of the actual true protein. Consequently, using conventional nitrogen to protein (N-P) conversion factor of 6.25, which is typically used in feed ingredient and feeds measurements would result in an overestimation of crude protein content of insect meals [177]. The latter is easily resolved as more appropriate N-P conversion factors for insect meals are now available [188,240–242]. Several papers investigated the use of food waste as insect rearing substrates with the dual purpose of decreasing food loss and waste and of obtaining valuable insect-derived proteins. However, like any farmed animals, insects also have specific nutritional requirements and research on this topic is fundamental for the formulation of specific diets able to fit the requirements[181,182,243–246]. Formulating specific diets for insects could enable to combine different waste in an optimal way, allowing the optimisation of cycles and productions.

Nowadays, the insect production is still very limited if compared to possible market share. Indeed, the current Europe insect protein production is estimated of about 5,000 tons[247]. Considering a global feed production of 1,235.5 million metric tons in 2021, of which aquaculture represents about 4.15%[248], to include 5 or 10% on insect meals in aquafeeds would require 2.57 and 5.14 million tons of product, respectively. Those values are far from being achieved even if the productions are booming also thanks to the growth in the number of producers and in their size. Today, the 54% of the insect production is used by the pet food market while only the 17% is devoted to aquaculture. However, a recent RaboBank report indicated a proportional increase of the aquafeed share up to 40% of the total by 2030[249] and an expected European total production capacity of 1 million metric tons[250]. Beside environmental benefits linked to their rearing on organic waste, their high feed conversion efficiency and their low green gas emissions and land use[251], insect production can also have positive social and economic impacts through the generation of new companies and jobs[250].

Under certain circumstance, related to the possible uptake of pathogens or undesirable compounds from the substrate (ex. dioxins, drugs), safety issues could arise. However, in addition to legislation in force in several producing countries that forbid the use of non-suitable substrates for insect rearing[252], risk could be mitigate by processing technologies using high temperatures both during insect meals and aquafeeds production[253].

Single-cell microorganisms

Humankind has been propagating microorganisms under varying degrees of controlled conditions for millennia and in applications such as food preservation and alcohol production. However, their mass cultivation and production into single-cell ingredients for use in industrial food and animal feed is a more recent endeavor [254–265], particularly within the context of a CBF. The use of single-cell ingredients for aquafeed applications is also not a new idea, as this has a long history. In fact, many of the microorganisms cultivated can no longer be considered ‘novel’, although new species and strains are emerging. However, the required ‘scale-up’ of such ingredients and the economic feasibility for commercial production has been limited until recently. Over the past decades, large research efforts have been made globally, both on laboratory-scale and pilot-scale, to re-examine opportunities, technical challenges, and the economic feasibility of up-scaling the production of single-cell ingredients like microalgae, cyanobacteria, protists, yeasts, and bacteria for use as sustainable alternatives to conventional aquafeed resources. To a large extent, developments and technological advancements have been driven by significant investments by the petrochemical industry, with the aim to either develop alternative biofuels (e.g., biodiesel, biogas, bioethanol, etc.) or to valorize refinery waste streams (e.g., carbon dioxide, methane, methanol, hydrogen, organic acids, etc.), with strategies to reduce their environmental footprint, meet their sustainability goals and commitments, diversify their product portfolios, and/or to maintain or grow company profits. As global climate change and industrial sustainability challenges continue, it is expected that these much-needed investments by the private and public sectors into the production of single-cell ingredients through a CBF will be sustained to help fuel the Blue Economy.

While cultivated for a wide variety of particular applications, essential nutrients, and bioactive compounds, what the microorganisms used to produce singe-cell ingredients all share is a vast genotypic and phenotypic diversity, a stunning capability to grow under extreme culture conditions (e.g., pH, salinity, temperature, irradiance, pollution load, etc.) on non-arable land, and with capacity for rapid growth on waste thermal energy and recycled nutrient substrates derived from industrial waste-streams and by-products [266–272]. Single-cell ingredients are also attractive alternatives to conventional terrestrial crop-based ingredients from a production standpoint as most can be intensively produced year-round, free from environmental stressors like seasonality, temperature fluctuations, unpredictable climatic condition, droughts or floods and invasive contamination, and their cultivation systems are amenable to a high degree of automation [273,274]. Not only do all these aforementioned characteristics of single-cell microorganisms provide important environmental services for society, they can also be simultaneously produced through industrial biotechnology for nutrient upcycling to transform waste streams into multiple value-added products; making single-cell ingredients ideal solutions under a CBF [28,273,275].

The aquafeed sector, in particular, is now greatly benefitting from these enhanced research efforts in recent years through accelerated bioprospecting and strain selection programs, rapid advances in cultivation, harvesting and down-stream processing technologies, and unprecedented access to biochemical characterization and nutritional quality data for a multitude of potential candidate microorganisms. The resulting so-called second generation single-cell ingredients (e.g., namely protein-rich meals, extracted oils and carotenoids) can have superior and 'tailorable' nutritional profiles compared to first generation terrestrial plant proteins, vegetable oils, predominantly used in modern aquafeeds. At the same time, increased use of single-cell ingredients is expected to pose fewer environmental sustainability concerns in regard to ecological conservation than terrestrial agriculture, such as freshwater use, deforestation, areal footprint and desertification, pesticide/fertilizer use, nutrient run-off, GHG emissions, and competition with human food resources. Thus, an ambitious and dedicated vision of Aquafeeds 3.0 presents a timely opportunity to 'de-couple' aquaculture's growing reliance on terrestrial agriculture, generate positive socioeconomic impacts, and further build aquaculture resiliency and social acceptability of sustainably farmed fish and shrimp. While the published literature over the past few decades is vast for every type, species, and strain of microorganism imaginable (from *Anabaena* to *Zymomonas*), the technical and economic challenges associated with the industrial-scale production have permitted only a small handful to reach the commercial aquafeed ingredient marketplace.

Production of single-cell ingredients

Production of single-cell ingredients from microorganisms involves primary cultivation, harvesting, and down-stream processing and these steps are largely defined by their taxonomy, biology, and physiological requirements of the individual microorganisms themselves and the intended final product(s)[276–278]. In a broad sense, microalgae and cyanobacteria are either cultivated under phototrophic conditions (e.g., natural or artificial light, pure or waste inorganic carbon, and inorganic nutrients), heterotrophic conditions (e.g., no light, organic carbon, and other organic and inorganic trace nutrients), or mixotrophic conditions (e.g., a combination of both strategies). As for cultivation technology intensity, they are generally mass-produced phototrophically, either outdoors in vast open or semi-closed ponds, raceways and sunlight-exposed flat-panel photobioreactors or indoors in highly-controlled enclosed photobioreactors. The major classes studied include the eukaryotic microalgae Chlorophyceae (green algae), Bacillariophyceae (diatomaceous algae) and Chrysophyceae (golden algae) and the prokaryotic cyanobacteria Cyanophyceae (blue-green algae)[279]. While there are over 200,000 known species of microalgae and cyanobacteria [280], the vast majority of species studied for use as aquafeed single-cell ingredients only include *Arthrospira* (Spirulina), *Chlorella*, *Crypthecodinium*, *Nannochloropsis*, *Phaeodactylum* and *Scenedesmus*; and to a lesser extent *Chlamydomonas*, *Desmodesmus*, *Entomoneis*, *Isochrysis*, *Nanofrustulum*, *Tetraselmis* and *Pavlova* [281–287]. On the other hand, protists, yeasts and bacteria are exclusively mass-cultivated heterotrophically indoors within highly-controlled bioreactors, commonly referred to as fermenters[288]. The major classes of these microorganisms that have been evaluated for use as aquafeed single-cellsingle-cell ingredients include marine protists like *Aurantiochytrium*, *Schizochytrium*, and *Thraustochytrium*, methanotrophic bacteria like *Methylobacterium* and *Methylococcus*, chemotrophic proteobacteria like *Clostridium* and *Baccillus*, and yeasts like *Candida*, *Cyberlindnera*, *Kluyveromyces*, *Rhodotorula*, *Saccharomyces*, and *Wickerhamomyces* [82,289–293]. Many of these studies have identified various nutrient-rich waste stream resources that can be used as media substrates to cultivate these microorganisms under a CBF for the production of single-cell ingredients include industrial flue or flare off-gases, municipal or industrial waste-waters, agricultural lignocellulosic crop or forestry biomass processing wastes, brewery and distillery by-products, terrestrial food/feed discards, and meat, seafood and aquaculture processing wastes, among others. With the industry still in its infancy and just now beginning to up-scale, global production data for single-cell ingredients for use in aquafeeds is difficult to quantify. However, a recent industry report[294] has identified twenty major producers of microalgae and cyanobacteria, and sixteen major producers of protists, yeasts and bacteria. The report further predicts that the production of aquafeed ingredients from single-cell microorganisms is poised to rapidly expand to commercially relevant scale that will likely outpace other alternative feed ingredients. Thus far, few producers have reached the large-scale production levels required for the aquaculture sector to meet the anticipated shortfall in seafood supply and demand in the coming decades; due predominantly to the high capital investments required to establish new facilities. That said, the report suggests that within 2-3 years, global production tonnage could exceed 700,000 tonnes.

Use of single-cell ingredients as sources of protein and/or lipid in fish and shrimp aquafeeds

A wide range of studies have evaluated the dietary inclusion of various single-cell ingredients in fish and shrimp aquafeeds and select examples of these can be viewed in the Supplementary Files (Supplementary Table S1 and S2). The references provided are not an exhaustive compendium of the published literature in this space and are limited to only those published within the past two decades. The use of most single-cell ingredients for bulk protein production has not yet achieved wide commercial success, due largely to prohibitively high production costs, and in some cases, palatability/digestibility/tolerance issues. The primary sources of protein used in modern aquafeeds such as fish meals, plant protein meals and concentrates, and rendered animal by-products, are generally in the pricing range of less than US$2 per kg, so alternatives will have to reach this pricing point to be realistic candidates for inclusion into the ingredient portfolio of commercial aquafeed manufacturers.. By contrast, the current cost of production for many single-cell ingredients is still higher and largely variable at US$4 to US$300 per kg depending upon species, production system and target products[284,295,296]. The cyanobacteria *Arthrospira* (Spirulina) and microalgae *Chlorella*, *Desmodesmus*, *Nannochloropsis*, *Phaeodactylum* and *Scenedesmus* are being mass-produced by multiple companies in many countries using outdoor ponds, raceways or flat panel bioreactors. Consequently, these are now being included in commercial aquafeeds to some extent. Due to comparatively low cell wall recalcitrance, acceptable inclusion levels of unprocessed *Arthrospira* (Spirulina) for most farmed fish and shrimp species is ~10-15%. By contrast, in the absence of energy-intensive and costly cell rupture processing, the maximum inclusion levels of most microalgae species are relatively low (~5-10%). Higher levels (e.g., up to 20%) appear to be possible following downstream processing steps like mechanical, chemical, or enzymatic cell rupture or extrusion pre-processing. A handful of methanotrophic bacterial single-cell protein (SCP) products are presently undergoing commercial scale-up and are expected to greatly impact the aquafeed protein ingredients market over the coming decade, particularly as economy-of-scale production costs continue to come down. These products are being produced exclusively indoors under heterotrophic fermentation by companies such as KnipBio, Calysta, Unibio, ADM, and Novonutrients among others. Significant inclusion levels are possible for several fish and shrimp species, although the published results regarding maximum acceptable levels are highly variable (e.g., less than 10% to over 35%) both between species and even within species from different studies. Dried powders and extracted oils rich in n-3 LC-PUFA (namely eicosapentaenoic acid, 20:5n-3, EPA and/or docosahexaenoic acid, 22:6n-3, DHA) derived from protists and marine microalgae like *Schizochytrium*, *Aurantiochytrium*, and *Crypthecodinium* have already been industrially-scaled by several companies (e.g., Alltech, Alganutra, Algarithm, Algorogin, ADM, Advanced BioNutrition, Bunge, Chambio, Corbion, DSM, Evonik, Fermentalg, Goerlich-Pharma, Kuehnle Agrosystems, Lyxia, Mara Renewables, Martek, Source-Omega, TerraVia and Verameris among others); many for the human food and supplement market but several with an aquafeeds focus. Originally, these products were mostly rich in DHA (lacking in EPA), but products rich in both n-3 LC-PUFA are now available and being used at significant inclusion levels in partial or complete displacement of FO in commercial fish and shrimp aquafeeds. As prices come down, these products have tremendous potential to sustainably advance aquaculture production and their high availability and recent industry uptake marks the beginning of a restoration of declining n-3 LC-PUFA levels in farmed fish and shrimp consumer products [289,297].

It is also prudent to note that some single-cell ingredients are also being employed for their carotenoids, both for tissue pigmentation and as potent dietary antioxidants. Algal induction of *Duneliella* and *Haematococcus* microalgae and fermentation of *Phaffia*/*Xanthophyllomyces* yeast and *Paracoccus carotinfaciens* bacteria are now at industrial-scale production by numerous companies (e.g., Algaetech, Algalif, AlgaTechnologies, Atacama, Beijing-Gingko, Cyanotech, Evergen, Jingzhou, Kuehnle Agrosystems, Kunming Biogenic, Nippon, Regenurex, Wefirst among others) for human health supplements but are also currently being used in commercial fish and shrimp aquafeeds as 'natural-source' alternatives to synthetic pigments, particularly astaxanthin [284]. The amount of dietary astaxanthin required for market-acceptable pigmentation of farmed fish and shrimp is very low (typically <80 mg/kg). As such, high inclusion levels of these products are unnecessary (generally <5% of the diet) provided that astaxanthin bioavailability is high. This does not appear to be an issue for oils and blended oleoresins extracted from single-cell microorganisms but most whole-cell powders generally require cell-rupture processing to ensure this; although weakened-cell wall strains and production systems are now in development [298]. Although these natural-source single-cell ingredients remain comparatively expensive relative to synthetic astaxanthin, they are increasingly in demand for sustainability purposes and for organic aquaculture product certification.

Perspectives

In the same manner as 2nd generation aquafeed ingredients (e.g., those derived from terrestrial crops), is it unlikely that any one 3rd generation single-cell ingredient will become a 'panacea' for most economically important farmed fish and shrimp species. Rather, it is anticipated that several select single-cell ingredients (along with other alternative feed ingredients discussed in this review) can be strategically selected and combined to provide a highly nutritious complement of essential nutrients that replicate conventional gold-standard 1st generation marine ingredients (e.g., FM and FO). As the technologies advance, production volumes grow and prices come down, it can be expected that several single-cell ingredients will gradually replace 2nd generation aquafeed ingredients as protein and lipid sources and, indeed, FM and FO as well. Furthermore, unlike 2nd generation ingredients used in today's modern aquafeeds; single-cell ingredients have a much greater capacity for tailored production through a CBF that increases the utilization of raw materials (e.g., industrial waste streams), decreases aerial land and potable water use, decreases the carbon footprint of aquafeed production, and enhances the overall sustainability and resiliency of fish and shrimp aquaculture. However, in order for Aquafeed 3.0 to be fully realized, these alternative ingredients must be available at prices that are competitive with established ingredients, they must possess functional attributes that do not impede the extrusion process and negatively affect pellet quality, and they need to be produced at large enough bulk scales to ensure consistent and predictable nutritional profiles at a stable and readily available supply to aquafeed manufacturers, and these barriers remain challenges for many single-cell ingredients. The published literature compiled for this section of the review (Supplementary Table S1 and S2) demonstrates that the majority of nutritional studies conducted so far with single-cell ingredients have focused on microalgae, cyanobacteria and protists, at least more so than bacteria and yeast at this point, although these too may have tremendous potential. In addition, most studies have focused on highly carnivorous species like salmonids and shrimps, and less on omnivorous species like tilapia and others. As discussed, several single-cell ingredients are now commercially available, and these are beginning to have positive impacts on enhancing aquafeed sustainability by reducing environmental footprint and ultimately helping to improve product quality, consumer and societal acceptance. Key examples highlighted in this section were sources of n-3 LC-PUFA-rich lipids from marine microalgae and protists and sources of essential amino acid (EAA) rich proteins from freshwater cyanobacteria and methanotrophic bacteria. While single-cell ingredients produced from some yeasts have shown potential for use as bulk protein sources, many species and strains have shown poor digestibility without significant downstream processing [299]. However, most yeast-derived products are currently used at low inclusion levels (rather than bulk proteins and lipids) either as natural-source astaxanthin for flesh pigmentation and as a dietary antioxidant or as a result of the fact that some of their intracellular or cell wall components (e.g., mannan oligosaccharides, nucleic acids and β-glucans) are proving effective at enhancing intestinal health and acting in a functional immunomodulatory role; both of which can enhance fish health and product quality for the consumer [300,301]. While other promising single-cell ingredients are currently under development utilizing newly isolated strains of bacteria, protists, microalgae, and yeast (particularly marine strains) that can be produced under a CBF, significant barriers like growth rate and productivity, cell-wall recalcitrance and innovative 'green' downstream processing requirements, and cost of production issues remain, and unprecedented global efforts are now resolving these challenges.

Macroalgae

Macroalgae (or seaweed) can be divided into three main groups: green (Chlorophyta), red, (Rhodophyta) and brown (Phaeophyta) algae. This highly taxonomically diverse group of aquatic organisms has long been investigated as a potential aquafeed ingredient due to their sustainability attributes. Furthermore, substantial quantities of macroalgae can be grown either at sea (e.g., long lines, rafts, and nets), or in land-based facilities (e.g., tanks and ponds). Depending on the species, the algae can be propagated by division and attached to the long lines (e.g., Eucheuma species) or tumble cultured. Alternatively, spores (gametophytes) are collected from the adult individuals and sprayed onto ropes and nets where they settle and are grown to harvestable size. Wild harvest macroalgae are also extensively carried out at scale for the functional polysaccharides- phycocolloids (e.g., agar, alginate, and carrageenan) production industry. Although, the quantities are limited because of their accessibility at the shoreline and legislative harvest restrictions to protect coastal habitats [302].

Much of the macroalgae aquaculture activities are in Asia, with China as the global lead producer with an annual reported harvest of over 25 million tonnes in 2020[3] . It has been estimated that over 80% of this production is used for human food, with the remainder used in animal feeds and other sectors[303]. For other nations, such as those found in Europe and Africa, there have been efforts in upscaling in commercial yields in the past decade (e.g., Norway, Faroe Islands, France, Ireland, and Russia). The cultivation of macroalgae has so far been limited to several species within the genera: *Undaria, Laminaria, Eucheuma, Pyropia* (previously designated within *Porphyra*), *Sargassum, Kappaphycus*, and *Gracilaria*, even though the latest taxonomic estimates suggest there are over 11,500 macroalgal species in the world: 2,000 brown, 7,500 red, and 2,000 green [304]. As such, there is substantial scope to diversify macroalgae aquaculture and its potential application for use in aquafeeds.

The domestication of seaweed has brought about a number of cultivars that have been selected for their profitable attributes, e.g., high yields, high-temperature resistance, and faster-growing characteristics. This has often been carried out through selective breedingand hybridization techniques in commercially important species: *Saccharina japonica* and *Undaria pinnatifida*. However, the resulting domestication has also led to concerns over the vulnerability of the algal germplasm stock being less diverse potentially leading to a decrease in favourable traits and susceptibility to extreme climate impact [305]. Most of the domestication of macroalgae has been concentrated in Asian countries such as China, Japan and South Korea. Furthermore, these producers often rely on wild populations for their annual seed (spore) stock [306]. Nevertheless, there is a need for safeguards to protect cultivated genetic stock, especially when growing the algae at sea where sporulation can occur and mix with wild populations, as evident in kelp species in the Far East [305]. The expansion of macroalgae production to meet aquafeed needs will also need to overcome the cultivation challenges such as diseases and pests[307]. Fungal, bacterial, and oomycete outbreaks can reduce the quality of the crop and production. For example, the oomycete pathogen *Olpidiopsis pyropia*has been estimated to reduce production output by 20% in Korean Pyropia (nori) farms[308]. Environmental changes can also induce diseases that can decrease quality and productivity, e.g., ice-ice disease. Epiphytic algae outbreaks such as the *Polysiphonia* species have been known to decrease *Kappaphycus* seaweed farms production from 1000 tonnes yr^{-1} to 100 tonnes yr^{-1}[309].

Macroalgae can play an important role in the circular seafood economy, especially exploiting their ability to capture dissolved nitrogenous waste residues from the water column, also, non-renewable, and anthropogenic macro-elements, such as phosphorus. In addition, anthropogenic nitrogen sources contribute to the eutrophication process. At the macroecological level, it has been estimated that China's macroalgae cultivation (inc. Undaria, Saccharina, and Pyropia) industry removes per annum, 75,000 tonnes of nitrogen and 9,500 tonnes of phosphorus from the country's coastal waters [310]. This ability to absorb significant amounts of nutrients could be exploited to manage wastewater produced from fish and shrimp farming production systems. For example, this is particularly relevant to intensively farmed fish (e.g., salmonids and tuna) land-based operations and recirculating aquaculture systems (RAS), where there is an opportunity to recapture nutrients. The integration of algae cultivation to an aquatic animal production system can mitigate the level of nutrients found in the system water, therefore reducing the need for system water exchange [311], and subsequently reduce water requirement and the environmental impact of the effluent discharge. Similarly, the concepts of polyculture and integrated multitrophic aquaculture systems also utilize seaweed to extract the nutrients from higher trophic levels species from the system, i.e., farmed fish[312]. Although these types of nutrient recycling strategies have so far been limited in their commercial deployment. This, often due to policy/legislative restraints (e.g., aquaculture licenses are not adapted for co-culture or fish disease outbreaks can prevent harvest and damage macroalgae crop), logistics (e.g., access of education (e.g., requirement of farmers to understand another species or demonstratable benefits), and lack of incentives (e.g., funding and greater requirement of investment and maintenance cost)[313]. Equally, the cultivation of macroalgae and use in aquafeeds could offer a means to reduce the environmental impact through atmospheric CO_2 capturing. The significance of such an effect has been estimated to be 2.48 million tonnes of CO_2 annum^{-1} being sequestered by the global macroalgae cultivation industry [314]. Or another example is for every tonne of harvested sugar kelp (*S. latissimi)*, 145 kg of CO_2 is captured [315]. With the continuing expansion of seaweed cultivation, this impact will be more and more significant. Moreover, in comparison to the use of terrestrial plant meals for aquafeed, the cultivation and expansion of using macroalgae in feeds do not displace significant amounts of arable land to achieve the carbon capture effect. The use of proteinaceous macroalgae feed ingredients could further bring down the overall environmental impact of aquafeed production to mitigate the effects of this expanding industry [316].

It should be noted that there is a need to consider the type of water body that the algae are grown in besides its nutritional composition. This is acute in kelp species where they are often known to bioaccumulate high levels of potentially toxic metals such as arsenic, mercury, cadmium, and lead [317]. The total element levels found in macroalgae can often exceed national and international legislative limits, e.g., EU Directive 2002/32/EC. Although, the level of concern remains somewhat unknown because many of these potentially toxic metals are often found to be bound to carbohydrates. Consequently, limiting the metal's toxicological effects, e.g., arsenosugars in kelps species [318]. When seaweed such as sugar kelp (*S. latissima*) was fed to rainbow trout potentially toxic metals: arsenic, cadmium, mercury, and lead did not affect the levels in the harvested fish fillets[319].

So far macroalgae have been exploited in several different forms in aquafeeds, such as dried and milled, refined, or as extracts of selected fractions. While the former requires low technology investment and knowledge and can produce the cheapest form of the feed ingredient, there are limitations of macroalgae products having an impact on the aquafeed formulation, i.e., as a protein and lipid nutrient source. This is because a large proportion of the seaweed is composed of carbohydrates, for example cellulose, hemicellulose, and complex polysaccharides (e.g., alginates, fucoidan, xylans, and carrageenans), ranging from 1.8 to 66% dry matter [320] of which are typically not well digested and nutritionally unavailable to many farmed fish, especially to carnivorous species. Increasing dietary inclusion levels to make up for the low protein content would only displace other ingredients where formulations for fish are highly conservative in terms of space for nutrient-dense diets. In general, past studies have shown that macroalgae can form 30% of a formulated feed composition without significant detriment to fish productivity indicators, e.g., growth performance and feed efficiency indices.

Biorefining methods such as the use of hydrolysis, extraction, and fermentation can all add value to the macroalgae through the reduction of the carbohydrate component and increase the bioavailability of the residual proteins. From an economic standpoint, this can dramatically add to the cost of the now proteinaceous macroalgae feed product and limit the cost-effectiveness needed to compete against other major proteins used in aquafeeds, such as soy protein concentrate [321]. However, the biorefining process might not be necessarily dedicated to fish feed production but come as a by-product from another production industry, such as biofuel generation that specifically requires the carbohydrate component or from the phycocolloid production, if the processes could be refined to preserve the protein and lipid constituents for feed use [322,323].

The use of macroalgae in aquafeeds can extend beyond the mere protein replacement by contributing functionality and bioactivity to fish and shrimp by interaction with the intestinal tract and related immune systems. The former is that the phycocolloids from the algae can replace traditional binders (e.g., gums, gluten, starches, and resin) used in the feed to create feed stability when the pellet sinks through the water column. Phytogenic and polysaccharide compounds in the algae can also confer bioactivity to the host organism by inducing the antioxidant defense mechanisms and systemic response via the mucosal barrier mechanism of the gut. This can have beneficial effects on skin and gill integrity that are affected by their systemic relationship. A metanalysis carried out on past research studies has shown that dietary macroalgae can enhance disease resistance and fish innate immunity through measured physiological and metabolic indicators, such as lysozyme, respiratory burst, chemolytic, and phagocytic activities [324]. Besides macroalgae offering immunomodulation benefits, these sustainable feed ingredients can also offer a means to deliver other functional benefits through flesh pigmentation, and antioxidative activity [319,325,326].

Therefore, macroalgae offer a diverse range of natural marine ingredients with unique characteristics and properties. Their potential inclusion in diets for farmed fish and crustacean species would add to our portfolio of sustainable raw materials, whilst adding value and enhancing food security and safety mainly via their functional role.

Consumer Perception and Acceptability

Consumer perception and acceptance of aquaculture products is critical to the success of the industry. The preference for wild fish over farmed fish is a well-known situation, and this can be more prevalent in some parts of the world than others[327], yet, several studies have also shown that consumers place more value in quality than production method (i.e., wild vs. farmed) [328,329]. Now more than ever, consumer awareness of responsible sourcing of products is at an all-time high. For example, awareness and growing concern over using soy products from the Amazon rainforest in Brazil (the world's leading soybean producer which has led to growing pressure on governments like the European Union to limit its use[330]. With soybean meal as the leading alternative to fishmeal in aquafeeds, there are concerns about its use in aquaculture in the future. That said, any novel ingredients that have potential in aquafeeds will be under public scrutiny, such as those described in this review. Knowledge on consumer attitudes towards utilizing novel ingredients sourced in the CFB is still growing. It has been shown that 73% of consumers across 71 countries in the UK, EU, and Asia were willing to eat fish, chickens, or pork from animals fed on a diet containing insect protein, and 80% wanted to know more about insect utilization [331]. Generally, most people recognized there was no or low risk to human health in eating farmed animals fed insect meal. However, consumer knowledge of the basic principle of scavenger ecology, and its role in the CFB, has yet to be explored, and may have challenges regarding acceptance and social license in aquaculture. The factors that determine whether consumers will buy into any novel feeds have been reported to mainly depend on the type of innovation and its market acceptance [332] .

Food safety, nutritional value, and sensory attributes are primary concerns of consumers regarding farmed fish, with diet being one of the reasons for these concerns. Several studies have investigated the impacts of novel ingredients (sourced from the CFB) on sensory perception and quality traits of the fish, as well as nutritional value. One of the most well studied examples regarding consumer acceptance and sensory perception is insect products, although even still, this area of research is still quite new. In general, analysis of sensory properties shows that there is no impact of these novel ingredients on fillet quality, perceived by untrained panelists as well as instrumental metrics (e.g., [180]). However, concerning meat and flesh quality, results are controversial, but a dramatic influence of nutritional value has been observed, such as the n-3 FA profile in salmon fed high inclusion levels of insect meals [180].

Consumer involvement plays a major role in the circular economy, which requires a new and more active role of consumers [333]. Consumer understanding, and possibly misunderstanding, of aquafeeds containing raw materials sourced from the CFB must be addressed prior to commercial use of Aqua 3.0

feeds. This could partially be addressed by ensuring product quality is the same, or better, in terms of sensory properties, since appearance is one of the first characteristics that consumers will encounter and make decisions on their purchase. Connecting consumer response with aquaculture is important, not only in terms of informing producers about consumer demands but also for marketing strategies [327]. Sensory information (e.g., organoleptic properties like texture, colour, and taste), as well as nutritional and safety information can be used as strategic tools to satisfy consumer demand and improve understanding of aquaculture products that had been fed diets containing ingredients sourced from the CFB.

Presumably, most consumers would agree with the principles of circularity, in terms of its potential for achieving food security in a sustainable manner. However, many consumers reject the notion of feeding 'byproducts' because they associate these feedstuffs with poor quality feeds, not appreciating that such ingredients provide nutritional and environmental performance value. Similarly, many consumers do not accept genetically modified organisms, despite evidence suggesting their role as a sustainable food source. This may present an issue with single celled organisms, which represent an opportunity to genetic alteration (e.g., to produce high levels of nutrients desirable in fish feeds). It is questionable whether consumers will accept these types of products, even if they are indirectly consumed (from feed to fish). Many consumers are increasingly aware of the need for greater environmental performance in aquafeeds, but they are not necessarily well-informed about different ingredients and their implications for sustainability in aquaculture. Embracing circularity in the production of blue foods requires the development of ingredients with the desired attributes as well as consumer education to support their adoption by the industry. Going forward, taking consumer perspective into account through active communication will integrate the consumer into the value creation process will improve value and consumer uptake[69]. Society needs to be made aware and encouraged to engage in the consumption of CFB-based products[69]. While consumer education will play an important role, price and consistently quality will highly influence purchasing habits.

Conclusion

Aquaculture must move towards a new paradigm where the carbon footprint and lower impacts on the environment are equal to production and profitability. Nutritional resources for aquaculture that are produced through a circular bioeconomy approach will allow for a new revolution, and a more resilient and sustainable aquaculture. Using a trophic level analogy, in the last 20 years, when aquafeeds evolved into "Aquafeed 2.0", farmed carnivorous species were shifted to become far more omnivorous than their natural diet. The sector is now further evolving into a more scavenger-based diet, which are essential in any healthy ecosystem, but currently missing in the global food system. This is shifting aquafeeds into a more modern "Aquafeed 3.0" platform. It is true that many of the suggested ingredients are already employed in the aquafeed industry (e.g., terrestrial animal by-products; fishery byproducts) but for moving toward the Aquafeed 3.0 concept, we must push these nutritional solutions further with advanced research and development. The circularity concept is not just limited to the examples in this review but there may be other options in the future, which must be assessed for their nutritional value and impacts on fish nutrition and health, but also must consider sustainability metrics, such as carbon footprint and energy use. However, circularity for ingredient production can also bring out safety issues and their use may be limited due to consumer perception and acceptability. Remedial methods to mitigate pathogens (bacteria, viruses, etc.) and past concerns of prions (PAPs) are a necessary prerequisite. To fully embrace circularity, future ingredients must be subjected to stringent regulatory frameworks for approval to use such ingredients in the next generation of aquafeeds. Additionally, it is of paramount importance to balance the need for rigor in these systems that are in place to prevent issues down the line, e.g., safety, pathogens, contaminants. Clean and biosecure sourcing and efficacy is warranted, including safety and compliance with international standards (FDA, EIFAC, CFIA, DEFRA, and global agencies). This is the opportunity for sustainable and resilient aquaculture, in the face of a changing climate, constantly turbulent economies, and rapidly evolving social dynamics and expectations, to produce healthy and nutritious seafood for all.

Acknowledgements

S.M. Colombo was supported by the Natural Science and Engineering Council of Canada Discovery Grant. She would also like to thank Zeyu Zhang with assistance in compiling references. Koushik Roy acknowledge the funds NAZV (QK22010177) for scoping alternative feed ingredients and future feeding strategies for Czech aquaculture. A.H.L Wan was co-funded under the Interreg Atlantic Area program through the EAPA_576/2018 NEPTUNUS project and the HYDROfish project (2019-2022) which was funded under the Disruptive Technologies Innovation Fund (DTIF), which is a €500 million fund established under Project Ireland 2040, run by the Department of Enterprise Trade and Employment with administrative support from Enterprise Ireland.

M. Overland was supported by Foods of Norway, a Centre for Research-based Innovation (the Research Council of Norway; Grant No. 237841/030).

Tables and Figures

Table 1 Points in future Circular Bioeconomy Framework (CBF) of food systems which could contribute to Aquafeed 3.0.

Point	Possible paths
Waste valorization within the food system and "up to farm".	Re-use (or, re-manufacture) of by-products from agriculture, livestock, forestry, and aquaculture farms.
	Sourcing feedstuffs from private brewery, bio-refinery, vermicomposting, insect cultivation, biofuel farms or retail chain food wastes which valorize wastes from any or all components of food systems.
Preventing losses "from farm to fork" by increasing utilization of non-food resources in production of high quality seafood	Low-cost value-added products from fish, livestock slaughter-house discards, culinary industries for the aquafeed industry.
	Targeting high value molecules/ bioactive compounds from bio-wastes and re-integration with aquafeed industry
Optimizing resource use efficiency *in-situ*	Live food generation by integrating trophic ecology, farm ecology, food web or multi-trophic culture, plankton ecology group model concepts.
	Farming of aquatic species at low trophic levels. For aquatic species at higher trophic levels, implementation of forage-fish based culture practices.
Optimizing resource use efficiency *in-vivo*	Identifying some locally available, circular origin feedstuffs which are data deficient, and their evaluation based on discussion with aquafeed industry stakeholders.
	Identifying feedstuffs, formulations derived from wastes that could complement and possibly lower the usage of present feedstuffs having high pressures on arable land, water, and biodiversity.

Colombo Stefanie (Orcid ID: 0000-0003-1828-7145)
Roy Koushik (Orcid ID: 0000-0001-7205-9034)
Mraz Jan (Orcid ID: 0000-0003-3545-1269)
Wan Alex H L (Orcid ID: 0000-0003-1703-3725)
Tibbetts Sean (Orcid ID: 0000-0001-5509-4081)
Øverland Margareth (Orcid ID: 0000-0003-1142-6624)
Metian Marc (Orcid ID: 0000-0003-1485-5029)

Fig. 1: A futuristic resource (e.g., nutrients) flow scheme and increased complexities in an aquaculture-centric food system adopting CBF for sustainably produced, circular-origin blue foods. Source: author [334].


Culture-based fisheries
(IMTA)
Forestry
Agriculture
Livestock
Waste recycling
Bio-Refinery
Planetary boundaries
Food system
Health boundaries
Pond fish farming
Recirculatory aquaculture system
Aquaponics
Biofloc

Colombo Stefanie (Orcid ID: 0000-0003-1828-7145)
Roy Koushik (Orcid ID: 0000-0001-7205-9034)
Mraz Jan (Orcid ID: 0000-0003-3545-1269)
Wan Alex H L (Orcid ID: 0000-0003-1703-3725)
Tibbetts Sean (Orcid ID: 0000-0001-5509-4081)
Øverland Margareth (Orcid ID: 0000-0003-1142-6624)
Metian Marc (Orcid ID: 0000-0003-1485-5029)

References

1. Harness the world's aquatic 'blue' food systems to help end hunger. *Nature* **597**, 303–303 (2021).

2. FAO Fisheries & Aquaculture. https://www.fao.org/fishery/en/global-search?q=statistics%20global-aquaculture-production%20en&lang=en (2022).

3. *In Brief to The State of World Fisheries and Aquaculture 2022*. (FAO, 2022). doi:10.4060/cc0463en.

4. Gephart, J. A. *et al.* Environmental performance of blue foods. *Nature* **597**, 360–365 (2021).

5. Tacon, A. G. J. & Metian, M. Feed matters: satisfying the feed demand of aquaculture. *Rev. Fish. Sci. Aquac.* **23**, 1–10 (2015).

6. Hua, K. *et al.* The future of aquatic protein: implications for protein sources in aquaculture diets. *One Earth* **1**, 316–329 (2019).

7. Naylor, R. L. *et al.* A 20-year retrospective review of global aquaculture. *Nature* **591**, 551–563 (2021).

8. Colombo, S. M. Chapter 2 - Physiological considerations in shifting carnivorous fishes to plant-based diets. in *Fish Physiology* (eds. Benfey, T. J., Farrell, A. P. & Brauner, C. J.) vol. 38 53–82 (Academic Press, 2020).

9. Fry, J. P. *et al.* Environmental health impacts of feeding crops to farmed fish. *Environ. Int.* **91**, 201–214 (2016).

10. Pahlow, M., van Oel, P. R., Mekonnen, M. M. & Hoekstra, A. Y. Increasing pressure on freshwater resources due to terrestrial feed ingredients for aquaculture production. *Sci. Total Environ.* **536**, 847–857 (2015).

11. Troell, M. *et al.* Does aquaculture add resilience to the global food system? *Proc. Natl. Acad. Sci.* **111**, 13257–13263 (2014).

12. Panserat, S., Marandel, L., Seiliez, I. & Skiba-Cassy, S. New insights on intermediary metabolism for a better understanding of nutrition in teleosts. *Annu. Rev. Anim. Biosci.* **7**, 195–220 (2019).

13. Colombo, S. M., Foroutani, M. B. & Parrish, C. C. Fats and oils in aquafeed formulations. in *Bailey's Industrial Oil and Fat Products* 1–28 (John Wiley & Sons, Ltd, 2020). doi:10.1002/047167849X.bio095.

14. Francis, G., Makkar, H. P. S. & Becker, K. Antinutritional factors present in plant-derived alternate fish feed ingredients and their effects in fish. *Aquaculture* **199**, 197–227 (2001).

15. Gatlin, D. M. *et al.* Expanding the utilization of sustainable plant products in aquafeeds: a review. *Aquac. Res.* **38**, 551–579 (2007).

16. Tacon, A. G. J., Metian, M. & McNevin, A. A. Future Feeds: Suggested Guidelines for Sustainable Development. *Rev. Fish. Sci. Aquac.* **30**, 135–142 (2022).

17. Froehlich, H. E., Gentry, R. R. & Halpern, B. S. Global change in marine aquaculture production potential under climate change. *Nat. Ecol. Evol.* **2**, 1745–1750 (2018).

18. Pernet, F. & Browman, H. I. The future is now: marine aquaculture in the anthropocene. *ICES J. Mar. Sci.* **78**, 315–322 (2021).

19. Barange, M. *et al.* Impacts of climate change on fisheries and aquaculture: synthesis of currrent knowledge, adaptation and mitigation options. *FAO Fish. Aquac. Tech. Pap. FAO Eng No 627* (2018).

20. Pörtner, H.-O. *et al.* The ocean and cryosphere in a changing climate. *IPCC Spec. Rep. Ocean Cryosphere Chang. Clim.* (2019).

21. Willett, W. *et al.* Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. *The Lancet* **393**, 447–492 (2019).

22. Maire, E. *et al.* Micronutrient supply from global marine fisheries under climate change and overfishing. *Curr. Biol.* **31**, 4132-4138.e3 (2021).

23. Laborde, D., Martin, W., Swinnen, J. & Vos, R. COVID-19 risks to global food security. *Science* **369**, 500–502 (2020).

24. Rumsey, G. L. History of Early Diet Development in Fish Culture, 1000 B.C. to A.D. 1955. *Progress. Fish-Cult.* **56**, 1–6 (1994).

25. *Fish nutrition*. (Elsevier, 2021).

26. Cottrell, R. S. *et al.* Time to rethink trophic levels in aquaculture policy. *Rev. Aquac.* **13**, 1583–1593 (2021).

27. European Commission. *EU Bioeconomy Strategy Progress Report*. https://ec.europa.eu/info/sites/default/files/research_and_innovation/research_by_area/documents/ec_rtd_eu-bioeconomy-strategy-progress.pdf (2022).

28. Colombo, S. M. & Turchini, G. M. 'Aquafeed 3.0': creating a more resilient aquaculture industry with a circular bioeconomy framework. *Rev. Aquac.* **13**, 1156–1158 (2021).

29. de Boer, I. J. & van Ittersum, M. K. *Circularity in agricultural production*. (2018).

30. Roy, K., Turkmen, S. & Turchini, G. M. Triggering circularity in aquaculture – an introductory virtual special issue. *Review in Aquaculture* https://onlinelibrary.wiley.com/page/journal/17535131/homepage/circularity-in-aquaculture-introduction (2021) doi:10.1111/(ISSN)1753-5131.

31. Commission, E. Food, Bioeconomy, Natural Resources, Agriculture and Environment. *European Commission - European Commission* https://ec.europa.eu/info/research-and-innovation/funding/funding-opportunities/funding-programmes-and-open-calls/horizon-europe/cluster-6-food-bioeconomy-natural-resources-agriculture-and-environment_en (2019).

32. Commission, E. *Food 2030 pathways for action: research and innovation policy as a driver for sustainable, healthy, and inclusive food systems*. (European Union Luxembourg, 2020).

33. Reike, D., Vermeulen, W. J. & Witjes, S. The circular economy: new or refurbished as CE 3.0?—exploring controversies in the conceptualization of the circular economy through a focus on history and resource value retention options. *Resour. Conserv. Recycl.* **135**, 246–264 (2018).

34. Muscat, A. *et al.* Principles, drivers and opportunities of a circular bioeconomy. *Nat. Food* **2**, 561–566 (2021).

35. Aschemann-Witzel, J. & Peschel, A. O. How circular will you eat? The sustainability challenge in food and consumer reaction to either waste-to-value or yet underused novel ingredients in food. *Food Qual. Prefer.* **77**, 15–20 (2019).

36. Aubin, J. *et al.* Implementing ecological intensification in fish farming: definition and principles from contrasting experiences. *Rev. Aquac.* **11**, 149–167 (2019).

37. Bodirsky, B. L. *et al.* Integrating degrowth and efficiency perspectives enables an emission-neutral food system by 2100. *Nat. Food* **3**, 341–348 (2022).

38. Campbell, B. M. *et al.* Agriculture production as a major driver of the Earth system exceeding planetary boundaries. *Ecol. Soc.* **22**, (2017).

39. Frehner, A. *et al.* The compatibility of circularity and national dietary recommendations for animal products in five European countries: a modelling analysis on nutritional feasibility, climate impact, and land use. *Lancet Planet. Health* **6**, e475–e483 (2022).

40. Gerten, D. *et al.* Feeding ten billion people is possible within four terrestrial planetary boundaries. *Nat. Sustain.* **3**, 200–208 (2020).

41. Girotto, F. & Piazza, L. Food waste bioconversion into new food: A mini-review on nutrients circularity in the production of mushrooms, microalgae and insects. *Waste Manag. Res.* **40**, 47–53 (2022).

42. Regueiro, L. *et al.* Opportunities and limitations for the introduction of circular economy principles in EU aquaculture based on the regulatory framework. *J. Ind. Ecol.* **n/a**, (2021).

43. Van Selm, B. *et al.* Circularity in animal production requires a change in the EAT-Lancet diet in Europe. *Nat. Food* **3**, 66–73 (2022).

44. WWF-WRAP. *Halving Food Loss and Waste in the EU by 2030: the major steps needed to accelerate progress*. 72 (2020).

45. Dagevos, H. & Lauwere, C. de. Circular Business Models and Circular Agriculture: Perceptions and Practices of Dutch Farmers. *Sustainability* **13**, 1282 (2021).

46. D'Abramo, L. R. & Zeigler, T. R. Development of aquafeeds: Reflections and future perspectives I. The foundational years: 1940-1979. *Aquafeed Adv. Process. Formul.* **14**, 39–43 (2022).

47. Naylor, R. L. *et al.* Effect of aquaculture on world fish supplies. *Nature* **405**, 1017–1024 (2000).

48. Kabir, K. A., Schrama, J. W., Verreth, J. A. J., Phillips, M. J. & Verdegem, M. C. J. Effect of dietary protein to energy ratio on performance of nile tilapia and food web enhancement in semi-intensive pond aquaculture. *Aquaculture* **499**, 235–242 (2019).

49. Kabir, K. A., Verdegem, M. C. J., Verreth, J. A. J., Phillips, M. J. & Schrama, J. W. Dietary non-starch polysaccharides influenced natural food web and fish production in semi-intensive pond culture of Nile tilapia. *Aquaculture* **528**, 735506 (2020).

50. Aubin, J., Papatryphon, E., van der Werf, H. M. G. & Chatzifotis, S. Assessment of the environmental impact of carnivorous finfish production systems using life cycle assessment. *J. Clean. Prod.* **17**, 354–361 (2009).

51. Biermann, G. & Geist, J. Life cycle assessment of common carp (Cyprinus carpio L.) – A comparison of the environmental impacts of conventional and organic carp aquaculture in Germany. *Aquaculture* **501**, 404–415 (2019).

52. Henriksson, P. J. G. *et al.* Product Carbon Footprints and Their Uncertainties in Comparative Decision Contexts. *PLOS ONE* **10**, e0121221 (2015).

53. Mungkung, R. *et al.* Life Cycle Assessment for environmentally sustainable aquaculture management: a case study of combined aquaculture systems for carp and tilapia. *J. Clean. Prod.* **57**, 249–256 (2013).

54. Papatryphon, E., Petit, J., Van der Werf, H. M. G. & Kaushik, S. J. *Life cycle assessment of trout farming in france: a farm level approach*. 71 (2004).

55. Bohnes, F. A., Hauschild, M. Z., Schlundt, J. & Laurent, A. Life cycle assessments of aquaculture systems: a critical review of reported findings with recommendations for policy and system development. *Rev. Aquac.* **11**, 1061–1079 (2019).

56. Newton, R. W. & Little, D. C. Mapping the impacts of farmed Scottish salmon from a life cycle perspective. *Int. J. Life Cycle Assess.* **23**, 1018–1029 (2018).

57. Pelletier, N. *et al.* Not all salmon are created equal: life cycle assessment (LCA) of global salmon farming systems. *Environ. Sci. Technol.* **43**, 8730–8736 (2009).

58. Boissy, J. *et al.* Environmental impacts of plant-based salmonid diets at feed and farm scales. *Aquaculture* **321**, 61–70 (2011).

59. Antony Jesu Prabhu, P. *et al.* Dietary ingredient composition alters faecal characteristics and waste production in common carp reared in recirculation system. *Aquaculture* **512**, 734357 (2019).

60. Kokou, F. & Fountoulaki, E. Aquaculture waste production associated with antinutrient presence in common fish feed plant ingredients. *Aquaculture* **495**, 295–310 (2018).

61. Tacon, A. G. J. Trends in Global Aquaculture and Aquafeed Production: 2000–2017. *Rev. Fish. Sci. Aquac.* **28**, 43–56 (2020).

62. Boyd, C. E. *et al.* Achieving sustainable aquaculture: Historical and current perspectives and future needs and challenges. *J. World Aquac. Soc.* **51**, 578–633 (2020).

63. Van Zanten, H. H. E. *et al.* Defining a land boundary for sustainable livestock consumption. *Glob. Change Biol.* **24**, 4185–4194 (2018).

64. Woodgate, S. L., Wan, A. H., Hartnett, F., Wilkinson, R. G. & Davies, S. J. The utilisation of European processed animal proteins as safe, sustainable and circular ingredients for global aquafeeds. *Rev. Aquac.* (2022).

65. Aspevik, T. *et al.* Valorization of proteins from co-and by-products from the fish and meat industry. *Chem. Chem. Technol. Waste Valorization* 123–150 (2017).

66. Damborg, V. K., Stødkilde, L., Jensen, S. K. & Weisbjerg, M. R. Protein value and degradation characteristics of pulp fibre fractions from screw pressed grass, clover, and lucerne. *Anim. Feed Sci. Technol.* **244**, 93–103 (2018).

67. Aiyar, A. & Pingali, P. Pandemics and food systems - towards a proactive food safety approach to disease prevention & management. *Food Secur.* **12**, 749–756 (2020).

68. Rohr, J. R. *et al.* Emerging human infectious diseases and the links to global food production. *Nat. Sustain.* **2**, 445–456 (2019).

69. Salvador, R. *et al.* Key aspects for designing business models for a circular bioeconomy. *J. Clean. Prod.* **278**, 124341 (2021).

70. Gray, R. S. & Torshizi, M. Update to agriculture, transportation, and the COVID-19 crisis. *Can. J. Agric. Econ. Can. Agroeconomie* **69**, 281–289 (2021).

71. Blanco, M., Sotelo, C. G., Chapela, M. J. & Pérez-Martín, R. I. Towards sustainable and efficient use of fishery resources: present and future trends. *Trends Food Sci. Technol.* **18**, 29–36 (2007).

72. Ramakrishna, R., Shipton, T. A., Hasan, M. R. & Food and Agriculture Organization of the United Nations. *Feeding and feed management of Indian major carps in Andhra Pradesh, India*. (Food and Agriculture Organization of the United Nations, 2013).

73. Wong, M. H., Mo, W. Y., Wai-Ming, C., Cheng, Z. & Man, Y. B. Recycle food wastes into high quality fish feeds for safe and quality fish production. *Environ. Pollut.* **219**, 631–638 (2016).

74. Jaffa, M. R. The use of bakery wastes as a nutritional source for fish. (Aston University, 1983).

75. Sorensen, M., Nguyen, G., Storebakken, T. & Overland, M. Starch source, screw configuration and injection of steam into the barrel affect the physical quality of extruded fish feed. *Aquac. Res.* **41**, 419–432 (2010).

76. Podoskina, T. A., Podoskin, A. G. & Bekina, E. N. Efficiency of utilization of some potato starch modifications by rainbow trout (Oncorhynchus mykiss). *Aquaculture* **152**, 235–248 (1997).

77. Evans, E. & Messerschmidt, U. Review: Sugar beets as a substitute for grain for lactating dairy cattle. *J. Anim. Sci. Biotechnol.* **8**, (2017).

78. San Martin, D. *et al.* Brewers' Spent Yeast and Grain Protein Hydrolysates as Second-Generation Feedstuff for Aquaculture Feed. *Waste Biomass Valorization* **11**, 5307–5320 (2020).

79. Revesz, N. *et al.* Protein replacement with dried distiller's grain with solubles (DDGS) in practical diet of common carp (Cyprinus carpio). *Aquac. Aquar. Conserv. Legis.* **12**, 1174–1188 (2019).

80. Estevez, A., Padrell, L., Inarra, B., Orive, M. & San Martin, D. Brewery by-products (yeast and spent grain) as protein sources in gilthead seabream (Sparus aurata) feeds. *Aquaculture* **543**, (2021).

81. Dawood, M. A. O. *et al.* Fruit processing by-products in the aquafeed industry: A feasible strategy for aquaculture sustainability. *Rev. Aquac.* (2022) doi:10.1111/raq.12680.

82. Agboola, J. O., Øverland, M., Skrede, A. & Hansen, J. Ø. Yeast as major protein-rich ingredient in aquafeeds: a review of the implications for aquaculture production. *Rev. Aquac.* **13**, 949–970 (2021).

83. Colombo, S. M., Zhang, Z., Wong, D. F. & Yuan, Z. Hydrolysis lignin as a multifunctional additive in Atlantic salmon feed improves fish growth performance and pellet quality and shifts gut microbiome. *Aquac. Nutr.* **26**, 1353–1368 (2020).

84. Yossa, R., Levesque, S., Groman, D. B. & Lora, J. H. Preliminary evaluation of purified lignin and hemicellulose as prebiotics candidates for Atlantic Salmon, *Salmo salar* L. *J. Appl. Aquac.* **30**, 256–271 (2018).

85. Tseng, M.-L., Chiu, A. S. F., Chien, C.-F. & Tan, R. R. Pathways and barriers to circularity in food systems. *Resour. Conserv. Recycl.* **143**, 236–237 (2019).

86. Turchini, G. M., Trushenski, J. T. & Glencross, B. D. Thoughts for the future of aquaculture nutrition: realigning perspectives to reflect contemporary issues related to judicious use of marine resources in aquafeeds. *North Am. J. Aquac.* **81**, 13–39 (2019).

87. Barton, P. S. & Evans, M. J. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. *Ecol. Entomol.* **42**, 364–374 (2017).

88. Wilson, E. E. & Wolkovich, E. M. Scavenging: how carnivores and carrion structure communities. *Trends Ecol. Evol.* **26**, 129–135 (2011).

89. Hill, J. E., DeVault, T. L., Beasley, J. C., Rhodes Jr, O. E. & Belant, J. L. Effects of vulture exclusion on carrion consumption by facultative scavengers. *Ecol. Evol.* **8**, 2518–2526 (2018).

90. Vicente, J. & VerCauteren, K. The Role of Scavenging in Disease Dynamics. in *Carrion Ecology and Management* (eds. Olea, P. P., Mateo-Tomás, P. & Sánchez-Zapata, J. A.) 161–182 (Springer International Publishing, 2019). doi:10.1007/978-3-030-16501-7_7.

91. Pereira, L. M., Owen-Smith, N. & Moleón, M. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Rev.* **44**, 44–55 (2014).

92. DeVault, T. L., Rhodes, J. & Shivik, J. A. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234 (2003).

93. Ben-David, M., Hanley, T. A., Klein, D. R. & Schell, D. M. Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. *Can. J. Zool.* **75**, 803–811 (1997).

94. Handler, K. S. *et al.* Temporal resource partitioning of wildebeest carcasses by scavengers after riverine mass mortality events. *Ecosphere* **12**, e03326 (2021).

95. Mateo-Tomás, P. *et al.* From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Divers. Distrib.* **21**, 913–924 (2015).

96. Jędrzejewski, W. & Jędrzejewska, B. Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Biatowieza National Park, Poland. *Ecography* **15**, 212–220 (1992).

97. Peers, M. J., Majchrzak, Y. N., Konkolics, S. M., Boonstra, R. & Boutin, S. Scavenging by Snowshoe hares (Lepus americanus) in Yukon, Canada. *Northwest. Nat.* **99**, 232–235 (2018).

98. Carter, D. O., Yellowlees, D. & Tibbett, M. Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften* **94**, 12–24 (2007).

99. Moleón, M., Sánchez-Zapata, J. A., Sebastián-González, E. & Owen-Smith, N. Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos* **124**, 1391–1403 (2015).

100. Moleón, M. *et al.* Carnivore carcasses are avoided by carnivores. *J. Anim. Ecol.* **86**, 1179–1191 (2017).

101. El-Sayed, A.-F. M. *Tilapia culture*. (Elsevier/Academic Press, 2020).

102. Dam, C. T. M. *et al.* Apparent digestibility of raw materials by yellowtail kingfish (Seriola lalandi). *Aquaculture* **511**, 734233 (2019).

103. Selva, N., Jedrzejewska, B., Jedrzejewski, W. & Wajrak, A. Scavenging on European bison carcasses in Bialowieza primeval forest (eastern Poland). *Ecoscience* **10**, 303–311 (2003).

104. Wilmers, C. C., Stahler, D. R., Crabtree, R. L., Smith, D. W. & Getz, W. M. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecol. Lett.* **6**, 996–1003 (2003).

105. Cortés-Avizanda, A., Selva, N., Carrete, M. & Donázar, J. A. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. *Basic Appl. Ecol.* **10**, 265–272 (2009).

106. FAO, F. The state of world fisheries and aquaculture 2020. Sustainability in action. *Rome* (2020).

107. Savoca, M. S. *et al.* Comprehensive bycatch assessment in US fisheries for prioritizing management. *Nat. Sustain.* **3**, 472–480 (2020).

108. Stevens, J. R., Newton, R. W., Tlusty, M. & Little, D. C. The rise of aquaculture by-products: Increasing food production, value, and sustainability through strategic utilisation. *Mar. Policy* **90**, 115–124 (2018).

109. Archer, M., Watson, R., Garret, A. & Large, M. *Strategic framework for seafood waste management*. (2005).

110. Nguyen, T. T., Zhang, W., Barber, A. R., Su, P. & He, S. Microwave-intensified enzymatic deproteinization of Australian rock lobster shells (Jasus edwardsii) for the efficient recovery of protein hydrolysate as food functional nutrients. *Food Bioprocess Technol.* **9**, 628–636 (2016).

111. Cretton, M., Malanga, G., Mazzuca Sobczuk, T. & Mazzuca, M. Lipid fraction from industrial crustacean waste and its potential as a supplement for the feed industry: a case study in argentine patagonia. *Waste Biomass Valorization* **12**, 2311–2319 (2021).

112. Mo, W. Y., Man, Y. B. & Wong, M. H. Use of food waste, fish waste and food processing waste for China's aquaculture industry: Needs and challenge. *Sci. Total Environ.* **613–614**, 635–643 (2018).

113. Aas, T. S., Ytrestøyl, T. & Åsgård, T. Utilization of feed resources in the production of Atlantic salmon (Salmo salar) in Norway: An update for 2016. *Aquac. Rep.* **15**, 100216 (2019).

114. Lionetto, F. & Esposito Corcione, C. Recent applications of biopolymers derived from fish industry waste in food packaging. *Polymers* **13**, 2337 (2021).

115. Paone, E. *et al.* Towards the anchovy biorefinery: biogas production from anchovy processing waste after fish oil extraction with biobased limonene. *Sustainability* **13**, 2428 (2021).

116. Abejón, R., Belleville, M. P., Sanchez-Marcano, J., Garea, A. & Irabien, A. Optimal design of industrial scale continuous process for fractionation by membrane technologies of protein hydrolysate derived from fish wastes. *Sep. Purif. Technol.* **197**, 137–146 (2018).

117. Ferraro, V. *et al.* Extraction of high added value biological compounds from sardine, sardine-type fish and mackerel canning residues — A review. *Mater. Sci. Eng. C* **33**, 3111–3120 (2013).

118. Okada, T. & Morrissey, M. T. Recovery and characterization of sardine oil extracted by pH adjustment. *J. Agric. Food Chem.* **55**, 1808–1813 (2007).

119. Egerton, S. *et al.* Replacing fishmeal with plant protein in Atlantic salmon (Salmo salar) diets by supplementation with fish protein hydrolysate. *Sci. Rep.* **10**, 4194 (2020).

120. Siddik, M. A. B., Howieson, J., Fotedar, R. & Partridge, G. J. Enzymatic fish protein hydrolysates in finfish aquaculture: a review. *Rev. Aquac.* **13**, 406–430 (2021).

121. Abdel-Ghany, H. M. & Salem, M. E.-S. Effects of dietary chitosan supplementation on farmed fish; a review. *Rev. Aquac.* **12**, 438–452 (2020).

122. Saini, R. K., Moon, S. H. & Keum, Y.-S. An updated review on use of tomato pomace and crustacean processing waste to recover commercially vital carotenoids. *Food Res. Int.* **108**, 516–529 (2018).

123. Routray, W., Dave, D., Cheema, S. K., Ramakrishnan, V. V. & Pohling, J. Biorefinery approach and environment-friendly extraction for sustainable production of astaxanthin from marine wastes. *Crit. Rev. Biotechnol.* **39**, 469–488 (2019).

124. Iizuka, A. *et al.* Recycling of shellfish wastes with a combined process of carbonate production and methane fermentation. *J. Chem. Eng. Jpn.* **42**, s43–s49 (2009).

125. Laso, J. *et al.* Achieving Sustainability of the Seafood Sector in the European Atlantic Area by Addressing Eco-Social Challenges: The NEPTUNUS Project. *Sustainability* **14**, 3054 (2022).

126. Toldrá, F., Mora, L. & Reig, M. New insights into meat by-product utilization. *Meat Sci.* **120**, 54–59 (2016).

127. World Bank. Meat processing and rendering. in *Pollution prevention and abatement handbook* 337–340 (The World Bank, 1998). doi:10.1596/0-8213-3638-X.

128. Marti, D. L., Johnson, R. J. & Mathews Jr, K. H. Where's the (not) meat? Byproducts from beef and pork production. *J. Curr. Issues Glob.* **5**, 397 (2011).

129. Hertrampf, J. W. & Piedad-Pascual, F. *Handbook on ingredients for aquaculture feeds*. (Springer Dordrecht, 2000).

130. Bellagamba, F., Caprino, F., Mentasti, T., Vasconi, M. & Moretti, V. M. The impact of processing on amino acid racemization and protein quality in processed animal proteins of poultry origin. *Ital. J. Anim. Sci.* **14**, 3770 (2015).

131. Meeker, D. L. & Hamilton, C. R. An overview of the rendering industry. *Essent. Render.* 1–16 (2006).

132. Li, M. H., Robinson, E. H. & Lim, C. E. Use of meatpacking by-products in fish diets. in *Alternative protein sources in aquaculture diets* (eds. Lim, C. E., Webster, C. D. & Lee, C. S.) 95–116 (The Haworth Press New York, NY, 2008).

133. Gasco, L. *et al.* Fishmeal alternative protein sources for aquaculture feeds. in *Feeds for the Aquaculture Sector: Current Situation and Alternative Sources* (eds. Gasco, L. et al.) 1–28 (Springer International Publishing, 2018). doi:10.1007/978-3-319-77941-6_1.

134. Oliva-Teles, A., Enes, P. & Peres, H. 8 - Replacing fishmeal and fish oil in industrial aquafeeds for carnivorous fish. in *Feed and Feeding Practices in Aquaculture* (ed. Davis, D. A.) 203–233 (Woodhead Publishing, 2015). doi:10.1016/B978-0-08-100506-4.00008-8.

135. Tacon, A. G. J., Hasan, M. R. & Metian, M. Demand and supply of feed ingredients for farmed fish and crustaceans: Trends and prospects. *FAO Fish. Aquac. Tech. Pap.* I,III,IV,VIII,IX,X,XI,XII,1-69,71-87 (2011).

136. NRA. Pocket information manual: a buyer's guide to rendered products. *Natl. Render. Assoc. Alex. VA* (2003).

137. Yu, Y. Replacement of fish meal with poultry by-product meal and hydrolyzed feather meal in feeds for finfish. in *Alternative protein sources in aquaculture diets* (eds. Lim, C. E., Webster, C. D. & Lee, C. S.) 51–93 (The Haworth Press New York, NY, 2008).

138. Riche, M. Nitrogen utilization from diets with refined and blended poultry by-products as partial fish meal replacements in diets for low-salinity cultured Florida pompano, Trachinotus carolinus. *Aquaculture* **435**, 458–466 (2015).

139. Ge, B. *et al.* Retrospective analysis of Salmonella, Campylobacter, Escherichia coli, and Enterococcus in animal feed ingredients. *Foodborne Pathog. Dis.* **10**, 684–691 (2013).

140. Rocker, M. M. *et al.* Poultry offal meal production conditions impact meal quality and digestibility in Atlantic salmon (Salmo salar). *Aquaculture* **542**, 736909 (2021).

141. Tacon, A. G., Metian, M. & Hasan, M. R. *Feed ingredients and fertilizers for farmed aquatic animals: sources and composition.* (Food and Agriculture Organization of the United Nations (FAO), 2009).

142. Heuzé, V. & Tran, G. Blood meal. *Feedipedia* (2016).

143. Campos, I., Pinheiro Valente, L. M., Matos, E., Marques, P. & Freire, F. Life-cycle assessment of animal feed ingredients: Poultry fat, poultry by-product meal and hydrolyzed feather meal. *J. Clean. Prod.* **252**, 119845 (2020).

144. Emery, J. A., Smullen, R. P. & Turchini, G. M. Tallow in Atlantic salmon feed. *Aquaculture* **422–423**, 98–108 (2014).

145. Rombenso, A. N., Turchini, G. M. & Trushenski, J. T. The omega-3 sparing effect of saturated fatty acids: A reason to reconsider common knowledge of fish oil replacement. *Rev. Aquac.* **14**, 213–217 (2021).

146. Bureau, D. P. & Meeker, D. L. Terrestrial animal fats. *Fish Oil Replace. Altern. Lipid Sources Aquac. Feeds CRC Press Boca Raton FL* 245–266 (2010).

147. Shirley, R. B. & Parsons, C. M. Effect of ash content on protein quality of meat and bone meal. *Poult. Sci.* **80**, 626–632 (2001).

148. Rombenso, A. N., Turchini, G. M. & Trushenski, J. T. The omega-3 sparing effect of saturated fatty acids: A reason to reconsider common knowledge of fish oil replacement. *Rev. Aquac.* **14**, 213–217 (2022).

149. Ockerman, H. W. & Hansen, C. L. *Animal by-product processing & utilization*. (CRC Press, 2000). doi:10.1201/9781482293920.

150. Dong, F. M. *et al.* Chemical composition and protein digestibility of poultry by-product meals for salmonid diets. *Aquaculture* **116**, 149–158 (1993).

151. Lewis, M. J. *et al.* A comparison of in-vivo and in-vitro methods for assessing the digestibility of poultry by-product meals using barramundi (lates calcarifer); impacts of cooking temperature and raw material freshness. *Aquaculture* **498**, 187–200 (2019).

152. Friedman, M. Chemistry, biochemistry, nutrition, and microbiology of lysinoalanine, lanthionine, and histidinoalanine in food and other proteins. *J. Agric. Food Chem.* **47**, 1295–1319 (1999).

153. Gilani, G. S., Cockell, K. A. & Sepehr, E. Effects of antinutritional factors on protein digestibility and amino acid availability in foods. *J. AOAC Int.* **88**, 967–987 (2005).

154. Batterham, E. S., Darnell, R. E., Herbert, L. S. & Major, E. J. Effect of pressure and temperature on the availability of lysine in meat and bone meal as determined by slope-ratio assays with growing pigs, rats and chicks and by chemical techniques. *Br. J. Nutr.* **55**, 441–453 (1986).

155. Bureau, D. Rendered products in fish aquaculture feeds. *Essent. Render. Anim. -Prod. Ind.* (2006).

156. Galkanda-Arachchige, H. S. C., Wilson, A. E. & Davis, D. A. Success of fishmeal replacement through poultry by-product meal in aquaculture feed formulations: a meta-analysis. *Rev. Aquac.* **12**, 1624–1636 (2019).

157. Lim, C., Webster, C. D. & Lee, C.-S. *Alternative protein sources in aquaculture diets*. (Haworth Press New York, 2008).

158. Trushenski, J. T. & Lochmann, R. T. Potential, implications and solutions regarding the use of rendered animal fats in aquafeeds. *Am. J. Anim. Vet. Sci.* **4**, 108–128 (2009).

159. Guo, J., Wang, Y. & Bureau, D. p. Inclusion of rendered animal ingredients as fishmeal substitutes in practical diets for cuneate drum, Nibea miichthioides (Chu, Lo et Wu). *Aquac. Nutr.* **13**, 81–87 (2007).

160. Sugiura, S. H., Dong, F. M., Rathbone, C. K. & Hardy, R. W. Apparent protein digestibility and mineral availabilities in various feed ingredients for salmonid feeds. *Aquaculture* **159**, 177–202 (1998).

161. El-Sayed, A.-F. M. Total replacement of fish meal with animal protein sources in Nile tilapia, Oreochromis niloticus (L.), feeds. *Aquac. Res.* **29**, 275–280 (1998).

162. Sullivan, J. A. & Reigh, R. C. Apparent digestibility of selected feedstuffs in diets for hybrid striped bass (Morone saxatilis ♀ X Morone chrysops ♂). *Aquaculture* **138**, 313–322 (1995).

163. Bureau, D. P., Harris, A. M. & Cho, C. Y. Apparent digestibility of rendered animal protein ingredients for rainbow trout (Oncorhynchus mykiss). *Aquaculture* **180**, 345–358 (1999).

164. Kirimi, J., Musalia, L., Magana, A. & Munguti, J. Performance of nile tilapia (Oreochromis niloticus) fed diets containing blood meal as a replacement of fish meal. *J. Agric. Sci.* **8**, p79 (2016).

165. Hatlen, B. *et al.* Growth performance, feed utilization and product quality in slaughter size Atlantic salmon (Salmo salar L.) fed a diet with porcine blood meal, poultry oil and salmon oil. *Aquac. Nutr.* **19**, 573–584 (2013).

166. Turchini, G. m. *et al.* Seven fish oil substitutes over a rainbow trout grow-out cycle: I) Effects on performance and fatty acid metabolism. *Aquac. Nutr.* **19**, 82–94 (2013).

167. Rao, M., Bast, A. & de Boer, A. Valorized food processing by-products in the EU: finding the balance between safety, nutrition, and sustainability. *Sustainability* **13**, 4428 (2021).

168. Henchion, M., McCarthy, M. & O'Callaghan, J. Transforming beef by-products into valuable ingredients: which spell/recipe to use? *Front. Nutr.* **3**, (2016).

169. Rozin, P. & Fallon, A. E. A perspective on disgust. *Psychol. Rev.* **94**, 23–41 (1987).

170. Gasco, L., Biancarosa, I. & Liland, N. S. From waste to feed: A review of recent knowledge on insects as producers of protein and fat for animal feeds. *Curr. Opin. Green Sustain. Chem.* **23**, 67–79 (2020).

171. Hua, K. A meta-analysis of the effects of replacing fish meals with insect meals on growth performance of fish. *Aquaculture* **530**, 735732 (2021).

172. Lock, E.-J., Biancarosa, I. & Gasco, L. Insects as raw materials in compound feed for aquaculture. in *Edible Insects in Sustainable Food Systems* (eds. Halloran, A., Flore, R., Vantomme, P. & Roos, N.) 263–276 (Springer International Publishing, 2018). doi:10.1007/978-3-319-74011-9_16.

173. Nogales-Mérida, S. *et al.* Insect meals in fish nutrition. *Rev. Aquac.* **11**, 1080–1103 (2019).

174. van Huis, A. Insects as food and feed, a new emerging agricultural sector: a review. *J. Insects Food Feed* **6**, 27–44 (2020).

175. Henry, M. A., Gai, F., Enes, P., Peréz-Jiménez, A. & Gasco, L. Effect of partial dietary replacement of fishmeal by yellow mealworm (Tenebrio molitor) larvae meal on the innate immune response and intestinal antioxidant enzymes of rainbow trout (Oncorhynchus mykiss). *Fish Shellfish Immunol.* **83**, 308–313 (2018).

176. Gasco, L., Józefiak, A. & Henry, M. Beyond the protein concept: health aspects of using edible insects on animals. *J. Insects Food Feed* **7**, 715–741 (2021).

177. Hawkey, K. J., Lopez-Viso, C., Brameld, J. M., Parr, T. & Salter, A. M. Insects: a potential source of protein and other nutrients for feed and food. *Annu. Rev. Anim. Biosci.* **9**, 333–354 (2021).

178. Oonincx, D. g. a. b. & Finke, M. d. Nutritional value of insects and ways to manipulate their composition. *J. Insects Food Feed* **7**, 639–659 (2021).

179. Jongema, Y. List of edible insects of the world (April 1, 2017). *WUR* https://www.wur.nl/en/Research-Results/Chair-groups/Plant-Sciences/Laboratory-of-Entomology/Edible-insects/Worldwide-species-list.htm (2017).

180. Gasco, L., Biasato, I., Dabbou, S., Schiavone, A. & Gai, F. Animals fed insect-based diets: state-of-the-art on digestibility, performance and product quality. *Animals* **9**, 170 (2019).

181. Barragan-Fonseca, K. B., Dicke, M. & van Loon, J. J. A. Influence of larval density and dietary nutrient concentration on performance, body protein, and fat contents of black soldier fly larvae (Hermetia illucens). *Entomol. Exp. Appl.* **166**, 761–770 (2018).

182. Bellezza Oddon, S., Biasato, I. & Gasco, L. Isoenergetic-practical and semi-purified diets for protein requirement determination in Hermetia illucens larvae: consequences on life history traits. *J. Anim. Sci. Biotechnol.* **13**, 17 (2022).

183. Taufek, N. M. *et al.* Apparent digestibility coefficients and amino acid availability of cricket meal, Gryllus bimaculatus, and fishmeal in African catfish, Clarias gariepinus, diet. *J. World Aquac. Soc.* **47**, 798–805 (2016).

184. Taufek, N. M. *et al.* Inclusion of cricket (Gryllus bimaculatus) meal in African catfish (Clarias gariepinus) feed influences disease resistance. *J. Fish.* **6**, 623–631 (2018).

185. Jeong, S.-M. *et al.* Nutritional evaluation of cricket, Gryllus bimaculatus, meal as fish meal substitute for olive flounder, Paralichthys olivaceus, juveniles. *J. World Aquac. Soc.* **52**, 859–880 (2021).

186. Tilami, S. K. *et al.* Insect meal as a partial replacement for fish meal in a formulated diet for perch Perca fluviatilis. *Turk. J. Fish. Aquat. Sci.* **20**, 867–878 (2020).

187. Jabir, M. A. R., Jabir, S. A. R. & Vikineswary, S. Nutritive potential and utilization of super worm (Zophobas morio) meal in the diet of Nile tilapia (Oreochromis niloticus) juvenile. *Afr. J. Biotechnol.* **11**, 6592–6598 (2012).

188. Fontes, T. V. *et al.* Digestibility of insect meals for nile tilapia fingerlings. *Animals* **9**, 181 (2019).

189. Alves, A. P. do C., Paulino, R. R., Pereira, R. T., da Costa, D. V. & e Rosa, P. V. Nile tilapia fed insect meal: Growth and innate immune response in different times under lipopolysaccharide challenge. *Aquac. Res.* **52**, 529–540 (2020).

190. Mikołajczak, Z., Rawski, M., Mazurkiewicz, J., Kierończyk, B. & Józefiak, D. The effect of hydrolyzed insect meals in sea trout fingerling (Salmo trutta m. trutta) diets on growth performance, microbiota and biochemical blood parameters. *Animals* **10**, 1031 (2020).

191. Karthick Raja, P., Aanand, S., Stephen Sampathkumar, J. & Padmavathy, P. Silkworm pupae meal as alternative source of protein in fish feed. *J. Entomol. Zool. Stud.* **7**, 78–85 (2019).

192. Freccia, A., Tubin, J. S. B., Rombenso, A. N. & Emerenciano, M. G. C. Insects in aquaculture nutrition: an emerging eco-friendly approach or commercial reality? in *Emerging Technologies, Environment and Research for Sustainable Aquaculture* 1–14 (IntechOpen London, UK, 2020).

193. Ravi, H. K. *et al.* Larvae mediated valorization of industrial, agriculture and food wastes: biorefinery concept through bioconversion, processes, procedures, and products. *Processes* **8**, 857 (2020).

194. Gasco, L. *et al.* Insect and fish by-products as sustainable alternatives to conventional animal proteins in animal nutrition. *Ital. J. Anim. Sci.* **19**, 360–372 (2020).

195. Pinotti, L. & Ottoboni, M. Substrate as insect feed for bio-mass production. *J. Insects Food Feed* **7**, 585–596 (2021).

196. Fowles, T. M. & Nansen, C. Insect-based bioconversion: value from food waste. in *Food Waste Management: Solving the Wicked Problem* (eds. Närvänen, E., Mesiranta, N., Mattila, M. &

Heikkinen, A.) 321–346 (Springer International Publishing, 2020). doi:10.1007/978-3-030-20561-4_12.

197. Sangiorgio, P. *et al.* Valorisation of agri-food waste and mealworms rearing residues for improving the sustainability of Tenebrio molitor industrial production. *J. Insects Food Feed* 1–16 (2021) doi:10.3920/JIFF2021.0101.

198. Ojha, S., Bußler, S. & Schlüter, O. K. Food waste valorisation and circular economy concepts in insect production and processing. *Waste Manag.* **118**, 600–609 (2020).

199. Sogari, G., Amato, M., Biasato, I., Chiesa, S. & Gasco, L. The potential role of insects as feed: a multi-perspective review. *Animals* **9**, 119 (2019).

200. van Huis, A. & Oonincx, D. G. A. B. The environmental sustainability of insects as food and feed. A review. *Agron. Sustain. Dev.* **37**, 43 (2017).

201. Allegretti, G., Talamini, E., Schmidt, V., Bogorni, P. C. & Ortega, E. Insect as feed: An emergy assessment of insect meal as a sustainable protein source for the Brazilian poultry industry. *J. Clean. Prod.* **171**, 403–412 (2018).

202. Smetana, S., Schmitt, E. & Mathys, A. Sustainable use of Hermetia illucens insect biomass for feed and food: Attributional and consequential life cycle assessment. *Resour. Conserv. Recycl.* **144**, 285–296 (2019).

203. Cadinu, L. A., Barra, P., Torre, F., Delogu, F. & Madau, F. A. Insect rearing: potential, challenges, and circularity. *Sustainability* **12**, 4567 (2020).

204. Barroso, F. G. *et al.* Insects as food: Enrichment of larvae of Hermetia illucens with omega 3 fatty acids by means of dietary modifications. *J. Food Compos. Anal.* **62**, 8–13 (2017).

205. Barroso, F. G. *et al.* Production of n-3-rich insects by bioaccumulation of fishery waste. *J. Food Compos. Anal.* **82**, 103237 (2019).

206. Danieli, P. P., Lussiana, C., Gasco, L., Amici, A. & Ronchi, B. The Effects of Diet Formulation on the Yield, Proximate Composition, and Fatty Acid Profile of the Black Soldier Fly (Hermetia illucens L.) Prepupae Intended for Animal Feed. *Animals* **9**, 178 (2019).

207. Ewald, N. *et al.* Fatty acid composition of black soldier fly larvae (Hermetia illucens) – Possibilities and limitations for modification through diet. *Waste Manag.* **102**, 40–47 (2020).

208. Liland, N. S. *et al.* Modulation of nutrient composition of black soldier fly (Hermetia illucens) larvae by feeding seaweed-enriched media. *PLOS ONE* **12**, e0183188 (2017).

209. Fuso, A. *et al.* Effect of the rearing substrate on total protein and amino acid composition in black soldier fly. *Foods* **10**, 1773 (2021).

210. Ravi, H. K. *et al.* Alternative solvents for lipid extraction and their effect on protein quality in black soldier fly (Hermetia illucens) larvae. *J. Clean. Prod.* **238**, 117861 (2019).

211. Caligiani, A. *et al.* Influence of the killing method of the black soldier fly on its lipid composition. *Food Res. Int.* **116**, 276–282 (2019).

212. Hashizume, A. *et al.* Housefly (Musca domestica) Larvae Preparations after Removing the Hydrophobic Fraction Are Effective Alternatives to Fish Meal in Aquaculture Feed for Red Seabream (Pagrus major). *Fishes* **4**, 38 (2019).

213. Bordignon, F. *et al.* Performance and fillet traits of rainbow trout (Oncorhynchus mykiss) fed different levels of Hermetia illucens meal in a low-tech aquaponic system. *Aquaculture* **546**, 737279 (2022).

214. Caimi, C. *et al.* First insights on black soldier fly (Hermetia illucens l.) larvae meal dietary administration in siberian sturgeon (Acipenser baerii brandt) juveniles. *Aquaculture* **515**, 734539 (2020).

215. Caimi, C. *et al.* Dietary inclusion of a partially defatted black soldier fly (Hermetia illucens) larva meal in low fishmeal-based diets for rainbow trout (Oncorhynchus mykiss). *J. Anim. Sci. Biotechnol.* **12**, 50 (2021).

216. Chemello, G. *et al.* Partially defatted tenebrio molitor larva meal in diets for grow-out rainbow trout, Oncorhynchus mykiss (Walbaum): effects on growth performance, diet digestibility and metabolic responses. *Animals* **10**, 229 (2020).

217. Dumas, A., Raggi, T., Barkhouse, J., Lewis, E. & Weltzien, E. The oil fraction and partially defatted meal of black soldier fly larvae (Hermetia illucens) affect differently growth performance, feed efficiency, nutrient deposition, blood glucose and lipid digestibility of rainbow trout (Oncorhynchus mykiss). *Aquaculture* **492**, 24–34 (2018).

218. Guerreiro, I. *et al.* Catching black soldier fly for meagre: Growth, whole-body fatty acid profile and metabolic responses. *Aquaculture* **516**, 734613 (2020).

219. Guerreiro, I. *et al.* Digestive enzyme activity and nutrient digestibility in meagre (Argyrosomus regius) fed increasing levels of black soldier fly meal (Hermetia illucens). *Aquac. Nutr.* **27**, 142–152 (2021).

220. Roncarati, A., Gasco, L., Parisi, G. & Terova, G. Growth performance of common catfish (Ameiurus melas Raf.) fingerlings fed mealworm (Tenebrio molitor) diet. *J. Insects Food Feed* **1**, 233–240 (2015).

221. Stejskal, V. *et al.* Partially defatted hermetia illucens larva meal in diet of eurasian perch (Perca fluviatilis) juveniles. *Animals* **10**, 1876 (2020).

222. Wang, G. *et al.* Evaluation of defatted black soldier fly (Hermetia illucens L.) larvae meal as an alternative protein ingredient for juvenile Japanese seabass (Lateolabrax japonicus) diets. *Aquaculture* **507**, 144–154 (2019).

223. Pulido, L. *et al.* Effect of dietary black soldier fly larvae meal on fatty acid composition of lipids and sn-2 position of triglycerides of marketable size gilthead sea bream fillets. *Aquaculture* **546**, 737351 (2022).

224. Tran, H. Q. *et al.* Production performance, nutrient digestibility, serum biochemistry, fillet composition, intestinal microbiota and environmental impacts of European perch (Perca fluviatilis) fed defatted mealworm (Tenebrio molitor). *Aquaculture* **547**, 737499 (2022).

225. Ido, A. *et al.* Replacement of fish meal by defatted yellow mealworm (Tenebrio molitor) larvae in diet improves growth performance and disease resistance in red seabream (Pargus major). *Animals* **9**, 100 (2019).

226. Li, Y. *et al.* Total replacement of fish meal with black soldier fly (Hermetia illucens) larvae meal does not compromise the gut health of Atlantic salmon (Salmo salar). *Aquaculture* **520**, 734967 (2020).

227. Mastoraki, M. *et al.* A comparative study on the effect of fish meal substitution with three different insect meals on growth, body composition and metabolism of European sea bass (Dicentrarchus labrax L.). *Aquaculture* **528**, 735511 (2020).

228. Rimoldi, S., Gini, E., Iannini, F., Gasco, L. & Terova, G. The effects of dietary insect meal from Hermetia illucens prepupae on autochthonous gut microbiota of rainbow trout (Oncorhynchus mykiss). *Animals* **9**, 143 (2019).

229. Rimoldi, S., Antonini, M., Gasco, L., Moroni, F. & Terova, G. Intestinal microbial communities of rainbow trout (Oncorhynchus mykiss) may be improved by feeding a Hermetia illucens meal/low-fishmeal diet. *Fish Physiol. Biochem.* **47**, 365–380 (2021).

230. Terova, G. *et al.* Effects of full replacement of dietary fishmeal with insect meal from Tenebrio molitor on rainbow trout gut and skin microbiota. *J. Anim. Sci. Biotechnol.* **12**, 30 (2021).

231. Weththasinghe, P. *et al.* Modulation of Atlantic salmon (Salmo salar) gut microbiota composition and predicted metabolic capacity by feeding diets with processed black soldier fly (Hermetia illucens) larvae meals and fractions. *Anim. Microbiome* **4**, 9 (2022).

232. Chemello, G. *et al.* Effects of Tenebrio molitor larvae meal inclusion in rainbow trout feed: myogenesis-related gene expression and histomorphological features. *Ital. J. Anim. Sci.* **20**, 1211–1221 (2021).

233. Terova, G., Ceccotti, C., Ascione, C., Gasco, L. & Rimoldi, S. Effects of partially defatted Hermetia illucens meal in rainbow trout diet on hepatic methionine metabolism. *Animals* **10**, 1059 (2020).

234. Weththasinghe, P., Hansen, J. Ø., Mydland, L. T. & Øverland, M. A systematic meta-analysis based review on black soldier fly (Hermetia illucens) as a novel protein source for salmonids. *Rev. Aquac.* **14**, 938–956 (2021).

235. Choi, I.-H. *et al.* Replacing fish meal by mealworm (*Tenebrio molitor*) on the growth performance and immunologic responses of white shrimp (*Litopenaeus vannamei*). *Acta Sci. Anim. Sci.* **40**, (2018).

236. Cummins, V. C. *et al.* Evaluation of black soldier fly (Hermetia illucens) larvae meal as partial or total replacement of marine fish meal in practical diets for Pacific white shrimp (Litopenaeus vannamei). *Aquaculture* **473**, 337–344 (2017).

237. Panini, R. L. *et al.* Potential use of mealworms as an alternative protein source for Pacific white shrimp: Digestibility and performance. *Aquaculture* **473**, 115–120 (2017).

238. Rahimnejad, S. *et al.* Replacement of fish meal with defatted silkworm (Bombyx mori L.) pupae meal in diets for Pacific white shrimp (Litopenaeus vannamei). *Aquaculture* **510**, 150–159 (2019).

239. Motte, C. *et al.* Replacing fish meal with defatted insect meal (yellow mealworm Tenebrio molitor) improves the growth and immunity of pacific white shrimp (Litopenaeus vannamei). *Animals* **9**, 258 (2019).

240. Boulos, S., Tännler, A. & Nyström, L. Nitrogen-to-protein conversion factors for edible insects on the swiss market: T. molitor, A. domesticus, and L. migratoria. *Front. Nutr.* **7**, (2020).

241. Janssen, R. H., Vincken, J.-P., van den Broek, L. A. M., Fogliano, V. & Lakemond, C. M. M. Nitrogen-to-protein conversion factors for three edible insects: Tenebrio molitor, Alphitobius diaperinus, and Hermetia illucens. *J. Agric. Food Chem.* **65**, 2275–2278 (2017).

242. Ritvanen, T., Pastell, H., Welling, A. & Raatikainen, M. The nitrogen-to-protein conversion factor of two cricket species - Acheta domesticus and Gryllus bimaculatus. *Agric. Food Sci.* **29**, 1–5 (2020).

243. Cohn, Z., Latty, T. & Abbas, A. Understanding dietary carbohydrates in black soldier fly larvae treatment of organic waste in the circular economy. *Waste Manag.* **137**, 9–19 (2022).

244. Gold, M. *et al.* Biowaste treatment with black soldier fly larvae: Increasing performance through the formulation of biowastes based on protein and carbohydrates. *Waste Manag.* **102**, 319–329 (2020).

245. Rumbos, C. I., Karapanagiotidis, I. T., Mente, E., Psofakis, P. & Athanassiou, C. G. Evaluation of various commodities for the development of the yellow mealworm, Tenebrio molitor. *Sci. Rep.* **10**, 11224 (2020).

246. Bellezza Oddon, S., Biasato, I., Resconi, A. & Gasco, L. Determination of lipid requirements in black soldier fly through semi-purified diets. *Sci. Rep.* **12**, 10922 (2022).

247. IPIFF. *The European insect sector today: challenges, opportunities and regulatory landscape. IPIFF vision paper on the future of the insect sector towards 2030*. (2019).

248. AllTech Agri-Food Outlook. *What does global feed production reveal about the future of agri-food?* https://www.alltech.com/agri-food-outlook (2022).

249. De Jong, B. & Nikolik, G. *No Longer Crawling: Insect Protein to Come of Age in the 2020s: Scaling up Is on the Horizon.* https://www.allaboutfeed.net/wp-content/uploads/2021/03/Rabobank_No-Longer-Crawling-Insect-Protein-to-Come-of-Age-in-the-2020s.pdf (2021).

250. IPIFF. *An overview of the European market of insects as feed. International Platform of Insects for Food and Feed*. https://ipiff.org/wp-content/uploads/2021/04/Apr-27-2021-IPIFF_The-European-market-of-insects-as-feed.pdf (2021).

251. Smetana, S., Spykman, R. & Heinz, V. Environmental aspects of insect mass production. *J. Insects Food Feed* **7**, 553–571 (2021).

252. Lähteenmäki-Uutela, A., Marimuthu, S. B. & Meijer, N. Regulations on insects as food and feed: a global comparison. *J. Insects Food Feed* **7**, 849–856 (2021).

253. Guiné, R. P. F., Correia, P., Coelho, C. & Costa, C. A. The role of edible insects to mitigate challenges for sustainability. *Open Agric.* **6**, 24–36 (2021).

254. Alaviuhkola, T., Korhonen, I., Partanen, J. & Lampila, M. Pekilo protein in the nutrition of growing-finishing pigs. *Acta Agric. Scand.* **25**, 301–305 (1975).

255. Atack, T. H., Jauncey, K. & Matty, A. J. The utilization of some single cell proteins by fingerling mirror carp (Cyprinus carpio). *Aquaculture* **18**, 337–348 (1979).

256. Beck, H., Gropp, J., Koops, H. & Tiews, K. Single cell proteins in trout diets. in *Finfish Nutrition and Feed Technology 2nd ed, Heenemann, Berlin, Germany* (eds. Halver, J. E. & Tiews, K.) 269–280 (FAO, 1979).

257. Bergstrom, E. Experiments on the use of single cell proteins in Atlantic salmon diets. in *FAO, Rome (Italy). Fisheries Dept. Symposium on Finfish Nutrition and Feed Technology. Hamburg (Germany, FR). 20 Jun 1978.* (1978).

258. Hepher, B., Sandbank, E. & Shelef, G. Alternative protein sources for warmwater fish diets. (1978).

259. Hoshiai, K. Protein aus petroleum. *Chem. Informationsdienst* **3**, no-no (1972).

260. Matty, A. J. & Smith, P. Evaluation of a yeast, a bacterium and an alga as a protein source for rainbow trout: I. Effect of protein level on growth, gross conversion efficiency and protein conversion efficiency. *Aquaculture* **14**, 235–246 (1978).

261. Roth, F. X. Microorganisms as a source of protein for animal nutrition. *Adv. Agric. Microbiol. NS Subba Rao* (1982).

262. Soeder, C. J. An historical outline of applied algology. in *CRC Handbook of Microalgal Mass Culture* (CRC Press, 1986).

263. Stringer, D. A. Industrial development and evaluation of new protein sources: Micro-organisms. *Proc. Nutr. Soc.* **41**, 289–300 (1982).

264. Vananuvat, P. & Balloun, S. L. Value of yeast protein for poultry feeds. *C R C Crit. Rev. Food Sci. Nutr.* **9**, 325–343 (1977).

265. Westlake, R. Large-scale continuous production of single cell protein. *Chem. Ing. Tech.* **58**, 934–937 (1986).

266. Adarme-Vega, T. C. *et al.* Microalgal biofactories: a promising approach towards sustainable omega-3 fatty acid production. *Microb. Cell Factories* **11**, 96 (2012).

267. Couture, J. L. *et al.* Environmental benefits of novel nonhuman food inputs to salmon feeds. *Environ. Sci. Technol.* **53**, 1967–1975 (2019).

268. Karimi, S., Mahboobi Soofiani, N., Mahboubi, A. & Taherzadeh, M. J. Use of organic wastes and industrial by-products to produce filamentous fungi with potential as aqua-feed ingredients. *Sustainability* **10**, 3296 (2018).

269. Spalvins, K., Zihare, L. & Blumberga, D. Single cell protein production from waste biomass: comparison of various industrial by-products. *Energy Procedia* **147**, 409–418 (2018).

270. Spalvins, K., Ivanovs, K. & Blumberga, D. Single cell protein production from waste biomass: review of various agricultural by-products. *Agron. Res.* **16**, 1493–1508 (2018).

271. Takors, R. *et al.* Using gas mixtures of CO, CO2 and H2 as microbial substrates: the do's and don'ts of successful technology transfer from laboratory to production scale. *Microb. Biotechnol.* **11**, 606–625 (2018).

272. Matassa, S. *et al.* Upcycling of biowaste carbon and nutrients in line with consumer confidence: the "full gas" route to single cell protein. *Green Chem.* **22**, 4912–4929 (2020).

273. Gupta, A., Barrow, C. J. & Puri, M. Multiproduct biorefinery from marine thraustochytrids towards a circular bioeconomy. *Trends Biotechnol.* **40**, 448–462 (2022).

274. Sharif, M. *et al.* Single cell protein: Sources, mechanism of production, nutritional value and its uses in aquaculture nutrition. *Aquaculture* **531**, 735885 (2021).

275. Campanati, C., Willer, D., Schubert, J. & Aldridge, D. C. Sustainable intensification of aquaculture through nutrient recycling and circular economies: more fish, less waste, blue growth. *Rev. Fish. Sci. Aquac.* **30**, 143–169 (2022).

276. Rebecca S. Thombre & Joshi, S. Industrial production and applications of yeast and yeast products. in *Industrial Biotechnology* 59–79 (2017).

277. Jacob-Lopes, E., Maroneze, M. M., Queiroz, M. I. & Zepka, L. Q. *Handbook of microalgae-based processes and products: fundamentals and advances in energy, food, feed, fertilizer, and bioactive compounds*. (Academic Press, 2020).

278. Akoijam, N., Kalita, D. & Joshi, S. R. Bacteria and Their Industrial Importance. in *Industrial Microbiology and Biotechnology* (ed. Verma, P.) 63–79 (Springer Singapore, 2022). doi:10.1007/978-981-16-5214-1_2.

279. Pal, R. & Choudhury, A. K. *An Introduction to Phytoplanktons: Diversity and Ecology*. (Springer India, 2014). doi:10.1007/978-81-322-1838-8.

280. Norton, T. A., Melkonian, M. & Andersen, R. A. Algal biodiversity. *Phycologia* **35**, 308–326 (1996).

281. Guedes, A. C., Sousa-Pinto, I. & Malcata, F. X. Chapter 8 - Application of Microalgae Protein to Aquafeed. in *Handbook of Marine Microalgae* (ed. Kim, S.-K.) 93–125 (Academic Press, 2015). doi:10.1016/B978-0-12-800776-1.00008-X.

282. Moomaw, W., Berzin, I. & Tzachor, A. Cutting Out the Middle Fish: Marine Microalgae as the Next Sustainable Omega-3 Fatty Acids and Protein Source. *Ind. Biotechnol.* **13**, 234–243 (2017).

283. Shah, M. R. *et al.* Microalgae in aquafeeds for a sustainable aquaculture industry. *J. Appl. Phycol.* **30**, 197–213 (2018).

284. Tibbetts, S. M. The potential for 'next-generation', microalgae-based feed ingredients for salmonid aquaculture in context of the blue revolution. in *Microalgal Biotechnology* (eds. Jacob-Lopes, E., Zepka, L. Q. & Queiroz, M. I.) (IntechOpen, 2018). doi:10.5772/intechopen.73551.

285. Ansari, F. A., Guldhe, A., Gupta, S. K., Rawat, I. & Bux, F. Improving the feasibility of aquaculture feed by using microalgae. *Environ. Sci. Pollut. Res.* **28**, 43234–43257 (2021).

286. Valente, L. M. P. *et al.* Chapter 9 - Microalgae as feed ingredients for livestock production and aquaculture. in *Microalgae* (ed. Galanakis, C. M.) 239–312 (Academic Press, 2021). doi:10.1016/B978-0-12-821218-9.00009-8.

287. Ahmad, A., W. Hassan, S. & Banat, F. An overview of microalgae biomass as a sustainable aquaculture feed ingredient: food security and circular economy. *Bioengineered* **13**, 9521–9547 (2022).

288. *Principles of Fermentation Technology*. (Elsevier, 2017). doi:10.1016/C2013-0-00186-7.

289. Sprague, M., Betancor, M. B. & Tocher, D. R. Microbial and genetically engineered oils as replacements for fish oil in aquaculture feeds. *Biotechnol. Lett.* **39**, 1599–1609 (2017).

290. Glencross, B. D., Huyben, D. & Schrama, J. W. The Application of Single-Cell Ingredients in Aquaculture Feeds—A Review. *Fishes* **5**, 22 (2020).

291. Jones, S. W., Karpol, A., Friedman, S., Maru, B. T. & Tracy, B. P. Recent advances in single cell protein use as a feed ingredient in aquaculture. *Curr. Opin. Biotechnol.* **61**, 189–197 (2020).

292. Jannathulla, R., Sravanthi, O., Moomeen, S., Gopikrishna, G. & Dayal, J. S. Microbial products in terms of isolates, whole-cell biomass, and live organisms as aquafeed ingredients: production, nutritional values, and market potential—a review. *Aquac. Int.* **29**, 623–650 (2021).

293. Nagappan, S. *et al.* Potential of microalgae as a sustainable feed ingredient for aquaculture. *J. Biotechnol.* **341**, 1–20 (2021).

294. Lux Research. *Future Fish Feed: Forecasting Alternative Aqua Feed Ingredients*. https://www.seafoodsource.com/news/aquaculture/new-report-explores-the-future-of-alternative-aquafeed-ingredients (2019).

295. Acién, F. G. *et al.* 20 - Economics of microalgae production. in *Microalgae-Based Biofuels and Bioproducts* (eds. Gonzalez-Fernandez, C. & Muñoz, R.) 485–503 (Woodhead Publishing, 2017). doi:10.1016/B978-0-08-101023-5.00020-0.

296. Ruiz, J., Wijffels, R. H., Dominguez, M. & Barbosa, M. J. Heterotrophic vs autotrophic production of microalgae: Bringing some light into the everlasting cost controversy. *Algal Res.* **64**, 102698 (2022).

297. Davis, D., Morão, A., Johnson, J. K. & Shen, L. Life cycle assessment of heterotrophic algae omega-3. *Algal Res.* **60**, 102494 (2021).

298. Hart, B. & Colombo, S. M. Effects of a novel weakened whole-cell form of Haematococcus pluvialis on flesh pigmentation of rainbow trout (Oncorhynchus mykiss) when compared to synthetic astaxanthin. *Aquac. Res.* **53**, 2408–2419 (2022).

299. Øverland, M., Karlsson, A., Mydland, L. T., Romarheim, O. H. & Skrede, A. Evaluation of Candida utilis, Kluyveromyces marxianus and Saccharomyces cerevisiae yeasts as protein sources in diets for Atlantic salmon (Salmo salar). *Aquaculture* **402–403**, 1–7 (2013).

300. Meena, D. K. *et al.* Beta-glucan: an ideal immunostimulant in aquaculture (a review). *Fish Physiol. Biochem.* **39**, 431–457 (2013).

301. Shurson, G. C. Yeast and yeast derivatives in feed additives and ingredients: Sources, characteristics, animal responses, and quantification methods. *Anim. Feed Sci. Technol.* **235**, 60–76 (2018).

302. Mac Monagail, M., Cornish, L., Morrison, L., Araújo, R. & Critchley, A. T. Sustainable harvesting of wild seaweed resources. *Eur. J. Phycol.* **52**, 371–390 (2017).

303. Packer, M. A., Harris, G. C. & Adams, S. L. Food and Feed Applications of Algae. in *Algae Biotechnology* (eds. Bux, F. & Chisti, Y.) 217–247 (Springer International Publishing, 2016). doi:10.1007/978-3-319-12334-9_12.

304. Guiry, M. D. & Guiry, G. M. AlgaeBase. World-wide electronic publication, National university of Ireland, Galway. (2021).

305. Hu, Z.-M. *et al.* Kelp aquaculture in China: a retrospective and future prospects. *Rev. Aquac.* **13**, 1324–1351 (2021).

306. Valero, M. *et al.* Perspectives on domestication research for sustainable seaweed aquaculture. *Perspect. Phycol.* **4**, 33–46 (2017).

307. Ward, G. M. *et al.* A review of reported seaweed diseases and pests in aquaculture in Asia. *J. World Aquac. Soc.* **51**, 815–828 (2020).

308. Kim, G. H., Moon, K.-H., Kim, J.-Y., Shim, J. & Klochkova, T. A. A revaluation of algal diseases in Korean Pyropia (Porphyra) sea farms and their economic impact. *ALGAE* **29**, 249–265 (2014).

309. Tsiresy, G. *et al.* Phenology of farmed seaweed Kappaphycus alvarezii infestation by the parasitic epiphyte Polysiphonia sp. in Madagascar. *J. Appl. Phycol.* **28**, 2903–2914 (2016).

310. Xiao, X. *et al.* Nutrient removal from Chinese coastal waters by large-scale seaweed aquaculture. *Sci. Rep.* **7**, 46613 (2017).

311. Neveux, N., Bolton, J. J., Bruhn, A., Roberts, D. A. & Ras, M. The bioremediation potential of seaweeds: recycling nitrogen, phosphorus, and other waste products. in *Blue Biotechnology* 217–239 (Wiley-VCH Verlag GmbH & Co. KGaA, 2018). doi:10.1002/9783527801718.ch7.

312. Chopin, T. & Tacon, A. G. J. Importance of Seaweeds and Extractive Species in Global Aquaculture Production. *Rev. Fish. Sci. Aquac.* **29**, 139–148 (2021).

313. Sickander, O. & Filgueira, R. Factors affecting IMTA (integrated multi-trophic aquaculture) implementation on Atlantic Salmon (Salmo salar) farms. *Aquaculture* **561**, 738716 (2022).

314. Duarte, C. M., Wu, J., Xiao, X., Bruhn, A. & Krause-Jensen, D. Can seaweed farming play a role in climate change mitigation and adaptation? *Front. Mar. Sci.* **4**, (2017).

315. Thomas, J.-B. E. *et al.* A comparative environmental life cycle assessment of hatchery, cultivation, and preservation of the kelp Saccharina latissima. *ICES J. Mar. Sci.* **78**, 451–467 (2021).

316. Seghetta, M., Hou, X., Bastianoni, S., Bjerre, A.-B. & Thomsen, M. Life cycle assessment of macroalgal biorefinery for the production of ethanol, proteins and fertilizers – A step towards a regenerative bioeconomy. *J. Clean. Prod.* **137**, 1158–1169 (2016).

317. Ratcliff, J. J. *et al.* Metal content of kelp (Laminaria digitata) co-cultivated with Atlantic salmon in an Integrated Multi-Trophic Aquaculture system. *Aquaculture* **450**, 234–243 (2016).

318. Rose, M. *et al.* Arsenic in seaweed—Forms, concentration and dietary exposure. *Food Chem. Toxicol.* **45**, 1263–1267 (2007).

319. Ferreira, M. *et al.* Diets supplemented with Saccharina latissima influence the expression of genes related to lipid metabolism and oxidative stress modulating rainbow trout (Oncorhynchus mykiss) fillet composition. *Food Chem. Toxicol.* **140**, 111332 (2020).

320. Wan, A. H. L., Davies, S. J., Soler-Vila, A., Fitzgerald, R. & Johnson, M. P. Macroalgae as a sustainable aquafeed ingredient. *Rev. Aquac.* **11**, 458–492 (2019).

321. Emblemsvåg, J. *et al.* Strategic considerations for establishing a large-scale seaweed industry based on fish feed application: a Norwegian case study. *J. Appl. Phycol.* **32**, 4159–4169 (2020).

322. Álvarez-Viñas, M., Flórez-Fernández, N., Torres, M. D. & Domínguez, H. Successful approaches for a red seaweed biorefinery. *Mar. Drugs* **17**, 620 (2019).

323. Baghel, R. S. *et al.* Seaweed biorefinery: A sustainable process for valorising the biomass of brown seaweed. *J. Clean. Prod.* **263**, 121359 (2020).

324. Thépot, V., Campbell, A. H., Rimmer, M. A. & Paul, N. A. Meta-analysis of the use of seaweeds and their extracts as immunostimulants for fish: a systematic review. *Rev. Aquac.* **13**, 907–933 (2021).

325. Valente, L. M. P. *et al.* Iodine enrichment of rainbow trout flesh by dietary supplementation with the red seaweed Gracilaria vermiculophylla. *Aquaculture* **446**, 132–139 (2015).

326. Moroney, N. C. *et al.* Influence of green seaweed (Ulva rigida) supplementation on the quality and shelf life of Atlantic salmon fillets. *J. Aquat. Food Prod. Technol.* **26**, 1175–1188 (2017).

327. Calanche, J. B., Beltrán, J. A. & Hernández Arias, A. J. Aquaculture and sensometrics: the need to evaluate sensory attributes and the consumers' preferences. *Rev. Aquac.* **12**, 805–821 (2020).

328. Vanhonacker, F., Altintzoglou, T., Luten, J. & Verbeke, W. Does fish origin matter to European consumers?: Insights from a consumer survey in Belgium, Norway and Spain. *Br. Food J.* **113**, 535–549 (2011).

329. Claret, A. *et al.* Consumer beliefs regarding farmed versus wild fish. *Appetite* **79**, 25–31 (2014).

330. Mempel, F. & Corbera, E. Framing the frontier – Tracing issues related to soybean expansion in transnational public spheres. *Glob. Environ. Change* **69**, 102308 (2021).

331. PROteINSECT. PROteINSECT: Insects as a sustainable source of protein. (2016).

332. Barrena, R. & Sánchez, M. Neophobia, personal consumer values and novel food acceptance. *Food Qual. Prefer.* **27**, 72–84 (2013).

333. Sijtsema, S. J., Snoek, H. M., van Haaster-de Winter, M. A. & Dagevos, H. Let's Talk about Circular Economy: A Qualitative Exploration of Consumer Perceptions. *Sustainability* **12**, 286 (2019).

334. Roy, K. Circular and sustainable fish nutrition. (University of South Bohemia in Ceske Budejovice, 2022).